BRITISH MUSEUM NATURAL HISTORY
PRESENTED
27 MAR 1951

BRITISH MUSEUM (NATURAL HISTORY)

Fossil Mammals of Africa

No. 1

THE MIOCENE HOMINOIDEA OF EAST AFRICA

W. E. LE GROS CLARK
and
L. S. B. LEAKEY

LONDON
1951

BRITISH MUSEUM (NATURAL HISTORY) — Geology [Vertebrata.]
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THE MIOCENE HOMINOIDEA OF EAST AFRICA

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With 9 plates and 28 figures in the text

LONDON
PRINTED BY ORDER OF THE TRUSTEES OF THE BRITISH MUSEUM

Issued March, 1951 *Price One Pound Five Shillings*

The Trustees of the British Museum have sanctioned the publication of a series of papers under the general title "Fossil Mammals of Africa". Each number will be issued separately.

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Note on the Material Described in this Number.

Specimens with a registration number following the initial M. are in the Department of Geology, British Museum (Natural History).

Specimens with numbers following the initials C.M.H. are in the Coryndon Museum, Nairobi (Hominoidea Collection).

Other specimens are referred to by the provisional numbers given to them in the field during each season's work of the British-Kenya Miocene Expedition; they will eventually be deposited either in the British Museum (Natural History) or in the Coryndon Museum.

Specimens with an S. number are from Songhor; those with an R. number, or not otherwise indicated, are from Rusinga.

PREFACE

The rich collections of fossil material made during recent years from Miocene deposits of East Africa contain numerous remains of primates of various types. Particularly important are those remains which, on the basis of their dental characters, are certainly to be regarded as anthropoid apes and which, therefore, come within the category of the Hominoidea. This monograph is concerned primarily with the specimens collected during 1947 and 1948 by the British-Kenya Miocene Expedition, but further studies have been made on the important material which had previously been found, and on which reports have already been published (Hopwood 1933, MacInnes 1943). We wish to express our gratitude for the opportunity of examining this earlier material, and we would particularly thank Dr. A. T. Hopwood for facilitating our study of the specimens in the British Museum, and for the advantage we have derived from discussing our new material with him. We are also much indebted to Professor D. M. S. Watson for advice, particularly on technical procedures in the graphic reconstruction of damaged specimens.

In this monograph our task, as we conceive it, is twofold, first, to present a general systematic account of all the hominoid fossils from East Africa which are so far available, and second, to indicate the general conclusions which, in our opinion, may reasonably be drawn from them regarding problems of the early evolution of the higher primates. We have not attempted to make an exhaustive analysis of all the material, which, in fact, is so plentiful that it would take a long time to collect all the comparative data necessary for such a treatment. On the other hand, some of the recent discoveries are so important and have aroused so much interest, that it is desirable to report on them without undue delay. For these reasons, some of our interpretations of the significance of the anatomical details in the skull, dentition, and particularly the limb bones, are necessarily provisional.

W. E. Le Gros Clark.
L. S. B. Leakey.

British Museum Natural History

I. THE DISCOVERY OF MIOCENE FOSSILS IN KENYA

The discovery of fossiliferous deposits of Miocene age in Kenya Colony was first made in 1909, when G. R. Chesnaye discovered a few fossils in the Muhoroni–Koru area east of Kisumu in the Kavirondo rift valley and, a month or two later, at Karungu on the eastern shore of Lake Victoria. These fossils were subsequently shown to C. W. Hobley, who was then Provincial Commissioner for Nyanza Province, and he arranged for a young Government Officer, D. B. Pigott, to search for further fossils at the Karungu exposures. Unfortunately this young man fell a victim to a crocodile, but not before he had collected a small series of fossils. Hobley sent the fossils obtained by Chesnaye and Pigott to C. W. Andrews of the British Museum, who published a short account of them in 1911.

In the winter of 1911 Felix Oswald visited East Africa on behalf of the British Museum in order to study the Karungu fossil beds, and to collect further specimens. The results of his expedition were very satisfactory and Oswald published (1914) an account of the geology of the Karungu beds, together with descriptions by C. W. Andrews and R. B. Newton of the Miocene fossils obtained.

It is known that C. W. Hobley visited Rusinga Island, at the mouth of the Kavirondo gulf, somewhere about 1913, in connection with the development of certain limestone deposits, but there is no available evidence to show that he discovered any fossils on the island, or that he realized that there were Miocene deposits there.

During 1926 and 1927 H. L. Gordon found numerous fossils on his farm at Koru and submitted some of them to E. J. Wayland, then Director of Geological Survey in Uganda. Wayland quickly realized their potential importance and encouraged Gordon to continue collecting. A year or two later he sent a selection of specimens from Koru to the British Museum (Natural History), where A. T. Hopwood recognized that these fossils were of comparable age with those described by Andrews from Karungu, and found among them the left maxilla of a large anthropoid ape. This was the first discovery of a Miocene hominoid in East Africa.

In 1931 Hopwood went to East Africa as a member of the third East African Archaeological Expedition and, while final arrangements were being made for the expedition to proceed to Olduvai Gorge, Tanganyika, he spent five weeks at Koru on behalf of the Trustees of the British Museum. During this period, nine further specimens representing fossil primates were recovered. He published a preliminary report on these primates in January 1933 and a more detailed study in November 1933. In these papers three new genera of Miocene hominoids, namely, *Proconsul*, *Limnopithecus*, and *Xenopithecus*, were described.

In the meantime, at the end of 1931 and again in 1932, L. S. B. Leakey and D. MacInnes, accompanied by several members of the third East African Archaeological Expedition, visited Rusinga Island. On the first visit, they discovered some Miocene beds rich in fossils which immediately yielded several hominoid remains. During 1932 also, Leakey and MacInnes discovered the Miocene beds at Songhor, north of

Muhoroni, and on the first visit to the site obtained two hominoids. At the same time, while on a visit to Rusinga Island, further fossiliferous Miocene beds were found on the adjoining island of Mwafangano. Some of the specimens obtained in 1931 and 1932 were examined by Sir Arthur Keith who provisionally ascribed them to the genus *Dryopithecus* (Keith, 1932).

In 1933 Archdeacon W. E. Owen, who had become interested in the Miocene, discovered a number of deposits at Ombo, Maboko Island, Mariwa, Majiwa, and Chianda Uyoma on the Kavirondo Gulf. MacInnes, in collaboration with Owen, undertook excavations at Maboko Island in 1934, with funds provided by the Royal Society. In 1933 also, Arambourg, while on his way back from the Omo fossil beds, discovered a fossiliferous Miocene site at Losodok, west of Lake Rudolf. He subsequently published a report on this site (1933). V. E. Fuchs and MacInnes visited the Losodok area in 1934.

In 1934 and 1935 Leakey took members of his fourth East African Archaeological Expedition to Rusinga Island, where P. E. Kent carried out a preliminary geological survey of the area. Once again, hominoid fossils were recovered. During the same season Kent also visited most of the other Miocene sites then known, and published a report in 1944.

At Songhor more hominoid material was found in 1934 and 1938 (MacInnes) and in 1940 and 1942 (Leakey). On Rusinga Island an almost complete mandible of *Proconsul* was found in 1942 (for a preliminary account see Leakey, 1943). This specimen will be referred to in this monograph as the 1942 mandible. The more important new Miocene primate specimens were briefly described by MacInnes (1943).

In 1944 R. M. Shackleton discovered a series of fossiliferous Miocene deposits south of Maralal, and these were described briefly in a report published by the Kenya Geological Survey in 1946. In 1944 F. Dixey, while on safari in the Lake Rudolf area, discovered some more Miocene fossil beds in the Loperot region (Dixey, 1944).

In February 1947 K. P. Oakley and Dorothea M. A. Bate of the British Museum (Natural History) and J. Waechter of Cambridge accompanied L. S. B. and Mary Leakey to Rusinga for a few days, when further important Miocene fossils were found.

Following upon the first Pan-African Congress of Prehistory, application was made to the Royal Society for funds to provide for a much more detailed study of the Kenya Miocene fossil beds. In July 1947 the *British-Kenya Miocene Expedition* started its first season's work upon Rusinga Island, with a grant from the Royal Society and a supplementary grant from H.H. the Aga Khan. During the season visits were also made to Mwafangano, Karungu, Koru, and Chianda Uyoma.

While collection and excavation were being carried out by MacInnes and L. S. B. and Mary Leakey, with the assistance of trained native staff, R. M. Shackleton and Ian Higginbottom undertook detailed geological mapping. The results of this first season's work exceeded expectations; no less than sixty-four specimens of Miocene primates were obtained, as well as several thousand specimens representing the associated fauna and flora.

At the close of the 1947 season Shackleton and MacInnes found an extension of the Songhor deposits in the Mtete Valley, and as a result of information supplied by

James Scott, visited Tambach, on the Elgeyo Escarpment, locating yet another fossiliferous Miocene deposit.

In February 1948 members of the University of California Expedition, who spent a few weeks working in the Losodok area, collected a number of Miocene fossils, including two specimens of hominoids. These were the first primate specimens to be discovered in the northern part of the Kenya Miocene deposits.

In June 1948, at the opening of the second season of the British-Kenya Miocene Expedition, financed this time by the Kenya Government and C. W. Boise, Leakey visited the Loperot site, discovered by Dixey, and ascertained that the exposures there were very extensive indeed, but that the probable cost of a prolonged expedition in this region would far exceed available funds. In July 1948 he found a new fossil site at Koru, some three miles distant from that found by Gordon and worked by Hopwood.

During the second half of August 1948 the British-Kenya Miocene Expedition established a camp at Songhor where, during the first eight weeks of work, seventy-seven more remains of Miocene primates were collected.

II. THE SITES WHICH HAVE YIELDED MIOCENE HOMINOID MATERIAL

Although the number of sites containing fossiliferous Miocene deposits now known in Kenya is large, not all of them have yielded specimens of Miocene primates. Those which have are Rusinga, Songhor, Koru, Maboko, Ombo, and Losodok.

Rusinga Island (text-fig. 1) is approximately ten miles in length, and the different sites on the island are so numerous that each main fossil area has been given a "sub-site" number. In the preliminary labels given to the specimens described in this monograph, the letter R indicates Rusinga, and S Songhor. The label Rs indicates a surface find and there necessarily remains an element of doubt concerning its exact origin. In those cases in which the letter R is not followed by a site number, the specimen is known to be derived from the Miocene deposits on Rusinga Island but its locality is not certainly known. The sub-sites which have yielded primate material, and which therefore concern us in this report, are chiefly concentrated on three different parts of the island, the first of these being in the neighbourhood of Hiwegi Hill, the second in the Kathwanga area and the third around Kiahera Hill. Three other sites on Rusinga Island have yielded primate material: Wakondu, Kalim, and the sub-site 113.

The sub-sites in the Hiwegi area (between Hiwegi Hill and the lake shore) which have yielded Miocene primates are R.1, R.A.1, R.1.A, R.3, R.17, and R.18. Each of these sub-sites is represented by a group of erosion gulleys cutting through sedimentary deposits which are in the main argillaceous. They were discovered in 1931, and have continued to yield important collections of fossils on every subsequent visit.

The sub-sites in the Kathwanga area which have yielded fossil primates are R.5, R.30, R.31, R.33, R.34, R.35, R.37, and R.39, all found during the 1931–32 season, and R.81 and R.91, found in the 1934–35 season.

The Kiahera sub-sites which have yielded Miocene primates are R.101, R.103, R.106, R.110, and R.112, all found during the 1934 and 1935 season, and R.106A site, as well as the site at the top of Kiahera Hill, found in 1947.

The Wakondu site was first found in 1947; it belongs to the same series of beds as those at R.2 and R.4 found in 1931. The beds at the sub-site R.4, which were found in 1931, and which have been later studied on several occasions, have not so far yielded any fossil primates. However, the discovery of a mandible of a primate at Wakondu, in exactly the same series of strata, suggests that the deposits at R.4 would be worth further study.

The age of the R.2 and R.4 and Wakondu beds in relation to those at Hiwegi, Kathwanga, and Kiahera cannot be stated until the geological results have been worked out.

The sub-site at R.113, which is not far from Kiahera Hill, was only discovered at the end of the 1947 season, and there is reason to believe that this particular sub-site, which yielded a maxilla of a juvenile hominoid (*Proconsul nyanzae*) and some other specimens, belongs to a series of deposits somewhat older than any of the others exposed on the island.

At Songhor the main site is small and has not been sub-divided. It has yielded a very large number of Miocene primates. There are two other minor sites at Songhor, which have yielded primate material, one in the Mtete Valley and the other below Sam Evan's house. At Koru the main site is that found by Gordon, and worked by Hopwood in 1931, while the second site is near the maize store at the other end of the farm situated there. The Maboko Island site lies in a narrow, shallow valley between the two higher portions of this small island; the deposits are not exposed naturally, but can only be seen by excavation. At Ombo the site is near the top of a cliff, just below an overlying lava-cap.

The only other site which has yielded Miocene primates is at Losodok; as already mentioned it was discovered by Arambourg, and it was briefly visited and worked in 1948 by the University of California Expedition. The area of Miocene beds exposed here is fairly large; the exact part of the site which yielded Miocene primate fossils is not known to us but will presumably be described in the report of the Expedition.

III. THE AGE OF THE MIOCENE BEDS

With the possible exception of the deposits on Maboko Island, the preliminary studies of the fossils from the beds which have yielded the Hominoidea described in this paper do not suggest any significant difference in the age of the various sites and horizons. The fossils collected at Karungu and described by C. W. Andrews were regarded by him as of Lower Miocene age because he considered *Deinotherium hobleyi* to be at the same stage of development as *D. cuvieri* of the European Burdigalian. The associated fauna as it was then known to him appeared to confirm that opinion. Hopwood found nothing in the fragmentary specimens from Koru to dissuade him

TABLE 1

PROVISIONAL LIST OF MAMMALIAN FOSSILS FROM EAST AFRICAN MIOCENE SITES

	Karungu	*Rusinga Island*	*Mfwangano*	*Chianda Uyoma*	*Ombo*	*Maboko Island*	*Songhor*	*Koru*	*Losodok*	*Loperot*	*Tambach*	*Maralal*
Proconsul	—	X	—	—	—	X	X	X	X	—	—	—
Limnopithecus	—	X	—	—	—	—	X	X	—	—	—	—
Sivapithecus	—	X	—	—	—	X	—	—	—	—	—	—
Mesopithecus ?	—	X	—	—	X	X	—	—	—	—	—	—
Progalago	—	X	—	—	—	—	X	X	—	—	—	—
INSECTIVORA	—	X	—	—	—	—	X	X	—	—	—	—
RODENTIA (several genera)	X	X	X	X	—	—	X	X	X	—	—	—
LAGOMORPHA (?2 genera)	—	X	—	X	—	—	X	—	—	—	—	—
Hyaenodon	—	X	—	—	X	X	—	—	—	—	—	—
Pterodon	—	X	—	—	—	X	—	—	—	—	—	—
Amphicyon	—	X	—	—	—	—	—	—	—	—	—	—
Pseudaelurus	X	—	—	—	—	—	—	—	—	—	—	—
Viverridae	—	X	—	—	—	—	—	—	—	—	—	—
Felidae	—	X	—	—	—	X	—	—	—	—	—	—
CARNIVORA indet.	X	X	—	—	X	X	X	X	—	—	—	—
Brachyodus	X	X	X	X	—	—	—	—	X	—	—	—
Hyoboops (*Merycops*)	X	X	—	—	X	—	—	—	—	—	—	—
Listriodon	—	X	—	—	—	X	—	—	X	—	—	—
SUIDAE indet.	—	X	—	—	X	X	X	X	—	—	—	—
TRAGULIDAE	X	X	X	X	X	X	X	X	X	X	—	—
Climacoceras	—	—	—	—	—	X	—	—	—	—	—	—
CHALICOTHERIIDAE	—	X	X	—	—	—	X	—	—	—	—	—
RHINOCEROTIDAE	X	X	—	X	X	X	X	—	X	X	X	—
Deinotherium	X	X	X	—	X	X	—	X	—	X	—	X
Trilophodon	X	X	—	X	X	X	X	—	X	—	—	X
Protanancus	—	—	—	—	—	X	—	—	—	—	—	—
Pliohyrax	—	X	—	—	—	—	X	—	X	—	—	—
Myohyrax	X	X	—	—	—	—	X	—	—	—	—	—
TUBULIDENTATA	—	—	X	—	—	—	—	—	—	—	—	—

In addition to the mammalian remains listed in broad outline above, the collections include numerous specimens of reptiles, fish, birds, crustaceans, myriapods, molluscs, and also important plant material.

from accepting Andrews' view; indeed, the primitive characters of the fossil primates appeared strongly to support it. Arambourg in his report on the small collection from Losodok (a site which has since yielded fossil primates of the *Proconsul* group) also accepted a Lower Miocene age for this series of deposits.

The richer and more abundant material which has since become available from Rusinga, Songhor, and elsewhere is now being studied in detail, and it is likely to provide more certain evidence for dating the deposits. While there seems no reason at present to alter the provisional estimate of early Miocene, it should be pointed out that this material includes some genera which, in other parts of the world, extend their range to horizons that are considerably younger than the Lower Miocene.

The accompanying faunal list contains at least six genera of which this is true. These genera are: *Amphicyon* (U. Olig.—L. Plio., Europe), *Pseudaelurus* (L.—U. Mioc., Europe) *Hyoboops* (L. Mioc.—L. Plio., Asia), *Listriodon* (L.—U. Mioc., Europe), *Deinotherium* (L. Mioc.—M. Plioc., Europe and Asia; L. Mioc.—Pleist., Africa), and *Trilophodon* (L. Mioc.—L. Plioc., Europe). In addition, three genera, *Sivapithecus, Mesopithecus,* and *Pliohyrax,* have not hitherto been recorded from horizons earlier than the Lower Pliocene. With regard to *Mesopithecus,* the material from Kenya has not yet been submitted to detailed analysis, but a preliminary examination of some of the specimens suggests that it is a more primitive type of cercopithecoid than the European form (and may in fact prove to be generically distinct). As regards *Pliohyrax,* the presence of this genus in the faunal list depends on Arambourg's determination of a single fragmentary mandible with two incomplete premolars from Losodok. The material now available includes nearly complete skulls and mandibles, the study of which may necessitate a different identification.

When considered in relation to the total assemblage, the presence in the Kenya Miocene beds of the genera just mentioned does not necessarily invalidate the estimate of Lower Miocene age. Nevertheless, taking all the evidence into account, we feel it desirable to emphasize that the early Miocene dating of the East African deposits is still in some sense provisional, and we are well aware that the critical studies now in progress may render necessary a certain amount of revision.

IV. THE MODE OF OCCURRENCE OF THE HOMINOID FOSSILS

The following analysis of the Miocene sites and sub-sites which have yielded fossil primates shows that there is a very great concentration of hominoid fossils at some of the sites. For example, the sub-site R.1 at Rusinga has yielded 18 specimens, sub-site R.106 15 specimens, and the quite small exposure at Songhor no less than 90 specimens.

It is not at all easy to understand how such concentrations of primates, often representing several genera and species, have come about in such relatively small areas. The specimens themselves are in every case broken and incomplete. The commonest specimens are pieces of mandibles and maxillae, or isolated teeth, with rare fragments of limb bones, and occasionally a complete talus or calcaneum. It seems fairly certain that all the fossils found represent bones washed into the lacustrine deposits, after the animals which they represent had been eaten by large carnivores, or perhaps by vultures and crocodiles. But, even so, the problem remains unsolved.

Clearly the primate population of the time was large, for the specimens found can only represent a minute portion of the total population. It seems possible, although by no means certain, that the hominoids of this period were very liable to the attacks of carnivora. The presence of the remains of so many individuals in shallow-water lacustrine deposits suggests, perhaps, that they were particularly vulnerable when they came down to the lake edge to drink, and that they were attacked and killed in large numbers under these conditions, so that the broken remains were washed into the lake beds from the adjoining shore at very frequent intervals. This would explain to some extent the concentration of specimens representing many individuals of several genera and species at more or less the same points, for, if we may draw an inference from the conditions round the African lakes to-day, there would be relatively few suitable watering points along the shore, thus making it necessary for the animals to go to these same places again and again.

What has been said about the primates applies equally to the other mammalian fossils: sites with a high concentration of primates invariably yield very numerous remains of other mammals such as hyracoids, rodents, tragulids, suids, and even such large animals as rhinoceroses. For example, the excavations at site R.1 on Rusinga Island which contained primate fossils also yielded within a few yards two partial rhinoceros skeletons, and remains of numbers of hyracoids, tragulids, and some rodents. Even sites which have so far yielded only a few primates nearly always show concentrations of other mammalian fossils.

So far as most of the animals are concerned, including the primates, the relative absence of even fragmentary limb bones in the deposits is exceedingly hard to explain. It is possible that, in view of their marrow content, the majority of such bones were actually broken up and eaten by the large hyaenodonts. The same explanation would account for the almost complete absence of skulls which, owing to their brain content, would be liable to be eaten by the larger carnivora, while mandibles and maxillae escaped this treatment and were merely broken up.

V. ANALYSIS OF THE DISTRIBUTION OF PRIMATE FOSSILS AT THE DIFFERENT SITES AND SUB-SITES

Table 2 does not represent every single specimen obtained. Where teeth were found in association, or where there was a reasonable probability that two or more specimens represent the same individual, they have been treated as a single specimen.

In addition to these, 10 hominoid specimens from Koru, described by Hopwood, and 2 hominoid specimens from Losodok, found by the University of California Expedition, must be added to the list.

Thus the total of Miocene fossil primate specimens from Kenya to date (22nd September, 1948) is 226 hominoids, 13 cercopithecids and more than 13 galagines. With the exception of two important specimens, this report only deals with material obtained before 22nd September, 1948. The exceptions are the skull of *Proconsul africanus* (R.1948, 50) from site R.106 and the mandible (R.1948, 375) found on the Lunene-Sienga ridge.

Table 2

TABLE SHOWING THE DISTRIBUTION OF MIOCENE PRIMATE FOSSILS

(*Based on specimens collected up to the end of September* 1948)

Site or Sub-site	*Hominoidea*	*Cercopithecidae*	*Galaginae*
Rusinga Sites & Sub-sites			
R.1 & R.A.1	18	3	—
R.1A	4	—	—
R.3	4	—	—
R.5	1	—	—
R.17	1	—	—
R.18	—	1	—
R.30	2	—	—
R.31	2	—	—
R.33	2	—	—
R.34	1	—	—
R.38	1	—	—
R.39	1	1	—
R.81	1	—	—
R.91	1	—	—
R.103	1	—	—
R.106	15	—	1
R.106A	8	—	—
R.112	1	—	—
R.113	5	—	—
Kiahera Hill	1	—	—
Kalim	1	—	—
Wakondu	1	—	—
Rusinga sundry surface sites	25	4	1
Kathwanga Rusinga surface site	12	—	—
Sites other than Rusinga :—			
Maboko Island	4	3	—
Ombo	1	1	—
Songhor (main site)	90	—	11
Songhor (Mtete Valley)	8	—	—
Koru	2	—	—
Total	214	13	13

VI. PROVISIONAL STRATIGRAPHICAL CLASSIFICATION OF FOSSILIFEROUS SITES AND STRATA ON RUSINGA ISLAND

The following is a list of the Miocene sites on Rusinga Island shown in the map (text-fig. 1); their provisional correlation with geological formations is indicated, the probable succession being based on the researches of R. M. Shackleton (1948, 1951) and

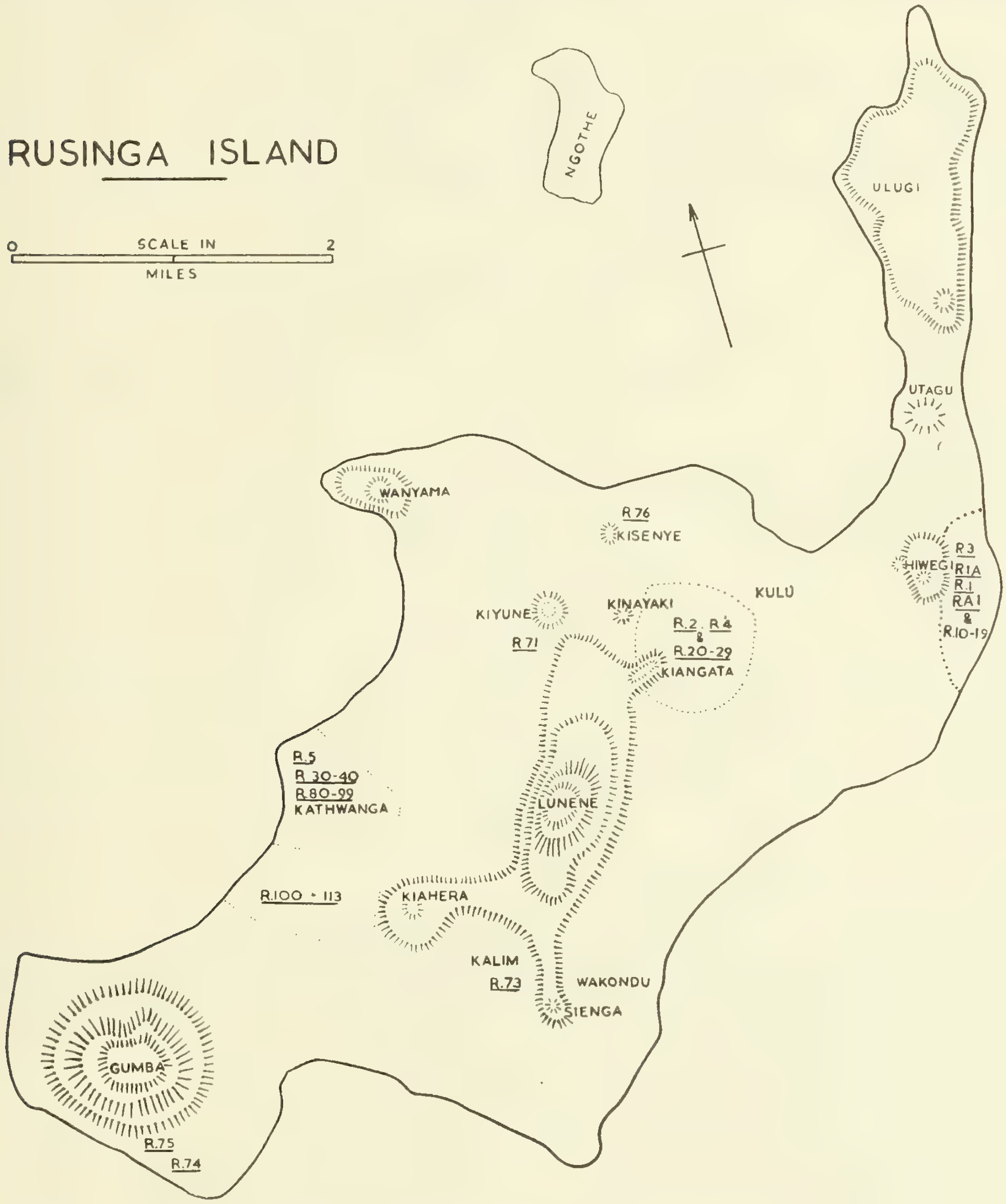

FIG. 1. Map of Rusinga Island showing fossil localities.

on unpublished work by I. Higginbottom. We have not attempted to make any stratigraphical correlation of the primate species, for the reason that the excavations in the area are still in progress and it is anticipated that much more material will be collected in the next few years.

R.1	Lower Hiwegi Beds.
R.1a	Lower Hiwegi Beds.
R.2	Kulu Series.
R.3	Upper Hiwegi Beds.
R.4	Kulu Series.
R.5	Red Band in upper part of Kathwanga Series.
R.10–19	Lower Hiwegi Beds.
R.20–29	Kulu Series.
R.30–40	Upper part of Kathwanga Series.
R.71	Lower Hiwegi Beds (?).
R.73	Kiahera Series.
R.74–75	Basal part of Kiahera Series.
R.76	Kiahera Series (?).
R.80–89	Lower part of Kathwanga Series.
R.100–112	Kiahera Series or lower part of Kathwanga Series.
R.113	Kiahera Series.
Kiahera Hill	Lower Hiwegi Beds.
Lunene-Sienga Ridge	Kiangata Agglomerate.
Utagu, E. of	Upper Hiwegi Beds.
Wakondu	Kulu Series.
Wanyama	Lower Hiwegi Beds.
Kalim	Kiahera Series.

The fossiliferous strata appear to be related as follows (I being the oldest):

IV	Kathwanga and Kulu Series.	
III	Hiwegi Series	Upper Hiwegi Beds (including Kiangata Agglomerate). Lower Hiwegi Beds.
II	Rusinga Agglomerate group.	
I	Kiahera Series.	

The relation of the Kulu Series to the Kathwanga Series is uncertain, but Shackleton infers that both are younger than the Hiwegi Series. Group IV also includes beds underlying the Kathwanga Series, named the Kathwanga Point Series, which have yielded no fossils apart from pieces of wood.

VII. DIAGNOSES

The fossil hominoid material from Kenya includes representatives of several genera and species; preliminary diagnoses of some species which had not previously been recognized were published in March 1950 (Le Gros Clark & Leakey). It will be found convenient if, before giving a detailed account of this material, the definitions of these categories are briefly stated. In regard to the genera *Proconsul* and *Limnopithecus*, and the species *P. africanus* and *L. legetet*, the original diagnoses given by Hopwood (1933) have been extended and amplified so as to render them applicable to the wider range of material now available, and also to take account of the degree of specific or generic variation indicated by this material.

Genus *PROCONSUL* Hopwood

Anthropoid apes showing considerable variation in size, ranging from animals smaller than a chimpanzee to animals the size of a gorilla. In the upper premolars (particularly $P\,\underline{3}$) the labial cusp tends to project well beyond the lingual cusp. Upper molars all characterized by a pronounced development of the internal cingulum which (particularly in the larger species) tends to be elaborately crenated. In $M\,\underline{1}$ and $M\underline{2}$ the trigon is clearly demarcated, and the hypocone is well developed. A protoconule is developed (to a variable degree) on the crest connecting the protocone to the paracone. There is usually a trace of the external cingulum. The last upper molar shows retrogressive changes, particularly in the smaller species. Lower molars showing the *Dryopithecus* pattern and with a distinct external cingulum. $M\,\overline{1}$ markedly smaller than $M\,\overline{2}$. $M\,\overline{3}$ elongated with a narrowing talonid. Upper central incisors spatulate and lacking the antero-posterior thickness of recent Ponginae. Incisor region of jaws narrow. Symphysis of mandible relatively massive, but lacking the simian shelf. Canines strongly developed (at least in the male), the upper being marked anteriorly by a deep vertical furrow (Le Gros Clark & Leakey, 1950, p. 260).

Proconsul africanus Hopwood

Holotype.—Portion of right maxilla with the upper dentition (Hopwood, 1933). Regd. M.14084 Brit. Mus. (N.H.) Geol. Dept.

Locality.—Koru.

A species of *Proconsul* intermediate in size between a large gibbon and a chimpanzee. Labial cusp of $P\,\underline{3}$ markedly projecting. Trigon particularly well defined by clear-cut crests. The main cusps of the trigon in the upper molars of about equal size. Hypocone approximating in size to the protocone. Protoconule only faintly indicated. Internal cingulum forming a rather prominent shelf, particularly anteriorly. Anterior cingulum well developed, posterior cingulum weak. Hypocone broadly continuous with internal cingulum in M $\underline{1}$ and M $\underline{2}$. M $\underline{3}$ much reduced in relative size, with considerable shrinkage of the metacone and hypocone. Total length of upper premolar-molar series less than 40 mm., and of lower series less than 45 mm. M $\overline{3}$ usually markedly elongated. Mandible strongly built but small, the maximum height of the body being less than 25 mm. The vertical ramus of the mandible is relatively low in comparison with the length of the body. Skull lightly constructed, with a narrow projecting muzzle, broad and relatively low orbits, and (at least in the female) no supra-orbital torus. The nasal aperture is narrowed below as in the Cercopithecidae, and the petrosal bone contains a well-developed subarcuate fossa (Le Gros Clark & Leakey, 1950, p. 260).

Proconsul nyanzae Le Gros Clark & Leakey

Holotype.—Maxilla and upper dentition (C.M.H.2), provisionally referred by MacInnes (1943) to *P. africanus*. Regd. M.16647 Brit. Mus. (N.H.) Geol. Dept.

Locality.—Rusinga.

A species of *Proconsul* approximating in size to a chimpanzee. Canines powerfully developed. In the upper molars the internal cingulum is elaborately beaded and forms a rounded rim on the inner surface of the crown. The anterior cingulum in feebly developed but the posterior cingulum is pronounced. Hypocone small in proportion to the protocone, and not broadly continuous with the internal cingulum in M $\underline{2}$. Protoconule forms a definite, rounded cuspule. M $\underline{3}$ not so markedly reduced as in *P. africanus*. Total length of upper premolar-molar series between 40 and 50 mm., of lower series between 45 and 55 mm. Mandible large and strongly built, the maximum depth of the body being about 35 mm., and the ascending ramus relatively high in comparison with the length of the body (Le Gros Clark & Leakey, 1950, p. 261).

Proconsul major Le Gros Clark & Leakey

Holotype.—Part of the right side of the mandible with the posterior premolar and all the molar teeth (S.80, 1947). Regd. M.16648 Brit. Mus. (N.H.) Geol. Dept.

Locality.—Songhor.

A species of *Proconsul* approximating in size to a gorilla. The lower teeth resemble those of *P. nyanzae* in their relative proportions and cusp pattern, but are of a much larger size. The total length of the lower premolar-molar series may be over 65 mm. The body of the mandible is massively constructed, with a maximum height reaching to more than 40 mm. (Le Gros Clark & Leakey, 1950, p. 261).

Genus *SIVAPITHECUS* Pilgrim

The diagnosis of this genus, as given by G. E. Lewis in his Taxonomic Syllabus of Siwalik Fossil Anthropoids (1937), is as follows: "Jaws and cheek-teeth medium large to very large in size. Molars moderately broad; crowns and robust cusps of medium height; labial and lingual cusps converge toward mid-line, greatest convergence lingual above and labial below. Upper dental arch with incisors separated from highly variable canines by a diastema. No diastemata in lower dental arch. Horizontal rami of medium depth." In addition, the genus differs from *Proconsul* in the absence of an internal cingulum in the upper molar teeth and in the relative simplicity of the cusp pattern.

Sivapithecus africanus Le Gros Clark & Leakey

Holotype.—Portion of left maxilla with the two premolars and the first molar (C.M.H.6), provisionally ascribed by MacInnes (1943) to *Proconsul.* Regd. M.16649 Brit. Mus. (N.H.) Geol. Dept.

Locality.—Rusinga.

Resembles the Indian species of *Sivapithecus* in the large size of the upper premolars, in the relative proportions of the main cusps of the upper molars, in the absence of a large posterior fovea, and in the clear separation of the hypocone from metacone and protocone. Differs from the Indian species of *Sivapithecus* in the flatness of the palate, in the development of the internal cingulum on $P\,\underline{4}$, and in the slightly narrower first and second upper molars (Le Gros Clark & Leakey, 1950, p. 261).

Genus *LIMNOPITHECUS* Hopwood

Small anthropoid apes approximating in size to the recent Hylobatinae. Upper molars of simple construction with a well-defined trigon, and a clearly demarcated hypocone continuous at its medial border with the internal cingulum. In the lower molars the cusps are in the form of conical tubercles surrounding a broad and shallow central basin. Well-developed hypoconulid. $P\,\overline{3}$ shows variable degrees of lateral compression (Le Gros Clark & Leakey, 1950, p. 261).

Limnopithecus legetet Hopwood
(including *L. evansi* MacInnes)

Holotype.—Portion of right side of mandible with first and second molars (Hopwood, 1933) Regd. M.14079 Brit. Mus. (N.H.) Geol. Dept.

Locality.—Koru.

A species of *Limnopithecus* approximating in size to *Hylobates.* Canines relatively small. Cusps of $P\,\underline{3}$ of approximately equal size. Internal cingulum of upper molars forms a narrow rim with no secondary elaborations. Distinct external cingulum in lower molars. Cusps of lower molars separated from each other by well-defined sulci. Anterior and posterior foveae feebly developed or absent. Mandible relatively robust. Total length of upper premolar-molar series (estimated) less than 25 mm., and of the lower series less than 30 mm. (Le Gros Clark & Leakey, 1950, p. 262).

Limnopithecus macinnesi Le Gros Clark & Leakey

Holotype.—The greater part of a mandible containing the premolar-molar series except for the first molar (710, 1947). Regd. M.16650 Brit. Mus. (N.H.) Geol. Dept.

Locality.—Rusinga.

A species of *Limnopithecus* approximating in size to *Symphalangus*. Upper canines strongly developed. Buccal cusp of $P\underline{3}$ elongated and sharply pointed. Upper molars of simple construction with a well-defined trigon and a relatively small hypocone. Internal cingulum forming a narrow rim with a slight indication of beading. Hypocone connected to metacone by a low crest. The main cusps of the lower molars similar to those of *L. legetet*, enclosing a broad talonid basin, but with a less distinct or absent external cingulum in $M\,\overline{2}$ and $M\,\overline{3}$. The protoconid and metaconid, and also the hypoconulid and entoconid, tend to be joined by well-marked crests. Anterior and posterior foveae relatively well developed. $P\,\overline{3}$ sharply compressed laterally. Mandible lightly constructed. Total length of upper premolar-molar series 25–30 mm., and of lower series 30 mm. or more (Le Gros Clark & Leakey, 1950, p. 262).

VIII. DETAILED DESCRIPTION OF THE MATERIAL

Proconsul africanus Hopwood, 1933

The holotype consists of part of a left maxilla from Koru (Brit. Mus. No. M.14084), with all the teeth except the incisors in position. The teeth are excellently preserved in this specimen and but slightly worn. Some of their main characters may be briefly noted here (Pl. 3, fig. 7; text-fig. 27). The upper canine is a stout pointed tooth, not markedly recurved, with a pronounced cingulum on the lingual side. Its anterior aspect is marked by a deep longitudinal groove. The anterior premolar is bicuspid, and distinguished by the relatively high and sharp-pointed labial cusp. In his diagnosis of the species, Hopwood included among the dental characters the fact that in the premolars the labial cusp is from 130 to 160 per cent. the height of the lingual cusp, and that the posterior cingulum is well marked. From the lateral view, the long slope of the anterior border of the labial cusp gives the third premolar a caniniform appearance (text-fig. 27). The transverse ridge connecting the two cusps lies close to the anterior margin of the crown of the tooth. The posterior upper premolar is distinctly smaller than the anterior, and differs also in the fact that the labial cusp is not so high. It is, however, larger than the lingual cusp. The transverse ridge connecting the two cusps is nearer the anterior than the posterior border of the crown; there is an anterior cingulum.

The upper molar teeth are characterized by the distinctness of the trigon, which is outlined by conspicuous sharply cut crests joining the main cusps. In relation to the crown as a whole, the trigon is relatively small, mainly because the internal cingulum is so strongly developed as to form a projecting ledge which appears to extend the occlusal surface. The internal cingulum forms a prominent, relatively broad shelf only a little below the level of the summits of the protocone and hypocone. All the molars have a weakly developed external cingulum. The enamel forming the floor of the trigon basin is relatively smooth. In the first two molars, the three cusps of the trigon are all of approximately equal bulk, and the hypocone is about equal in size to the protocone. The anterior cingulum is pronounced in all the molars, being particularly well developed in the first, and almost as distinct in the second. The second molar is conspicuously larger than the first, and the internal cingulum is more beaded. The hypocone is also relatively higher, and in this tooth is flanked by a weakly developed postero-internal cingulum which is not present in this position in the first molar. In both the first and second molars the hypocone is broadly continuous anteriorly with the internal cingulum. A small incipient cuspule, the protoconule, is faintly indicated at a slight forward angulation of the crest connecting the protocone with the paracone. The third molar is much reduced in size, and the metacone and hypocone are both small and indistinct, their apices being at a much lower level than the protocone and paracone. The ridge linking the latter two cusps shows a pronounced angulation as in the second molar. The internal cingulum is relatively wide and coarsely wrinkled.

The teeth in the holotype of *P. africanus* are relatively small in comparison with the size of the maxilla so far as this can be inferred from the rather small fragment of the bone which has been preserved. In its general dimensions the maxilla must have approached that of a chimpanzee. As Hopwood has pointed out, the root of the zygomatic process has its origin very close to the alveolar border, but its contour indicates that the process was strongly built. The mid-line of the palate is not preserved in the holotype, but measurements show that the width of the palate between the inner margins of the canines must have been about 22 mm., and between the inner margins of the first molars about 24 mm.

In addition to the holotype of *P. africanus*, Hopwood referred to the same species an isolated first upper molar (M.14085), a weathered third lower molar (M.14087), and a mandible with some of the teeth, much worn, in position (M.14086). For reasons which will be discussed later (see p. 47), there is now reason to suppose that the mandible must probably be referred to a different species (*P. nyanzae*).

THE SKULL OF *PROCONSUL AFRICANUS*—R.1948, 50 (R.106)

During the second season of the British-Kenya Miocene Expedition a very remarkable specimen was found, namely, a skull of *P. africanus*. Since this is the first skull of a Miocene ape to be found anywhere, it is clearly of outstanding importance. The discovery was made on 2nd October, initially by Mrs. Leakey. While exploring a steep face of one of the gullies on Rusinga Island near R.106 and R.106A, she noticed some small skull fragments washed out on the slope. Following up this discovery, she found an upper third molar of *Proconsul* and called the attention of her husband. On cutting back into the beds, most of the rest of the skull was brought to light, consisting of the greater part of the facial skeleton (well preserved on the right side but much crushed and broken on the left side), the frontal region of the roof of the skull, detached parts of the occipital bone, a practically complete mandible (warped on the left side), and numerous small isolated pieces including fragments of the petrosal bones. The upper and lower dentitions are excellently preserved in their entirety in this fine specimen. The last molars had erupted and show a very slight degree of wear. Clearly, therefore, the skull belonged to a young adult. The specimen required extreme care in its removal, and by close and patient study it was possible to piece together some of the small detached fragments and replace them in their proper position in the skull.

The appearance of the fossil skull from different points of view is shown in Pls. 1 and 2, figs. 1–4, and in text-figs. 2–4 an attempt has been made to represent the complete skull as it would have appeared in an undamaged condition. The latter figures were carefully drawn to scale, and corrections for distortion were made by reference to direct measurements of the actual specimen. By reconstructing on squared paper different views of the skull independently (orientated on the plane of the occlusal surface of the cheek teeth), and also the palate and mandible, and checking one against another, it is believed that these illustrations reproduce fairly closely the appearance of the intact skull, but in any case they are to be regarded as approximations only. This particularly applies, of course, to those parts of the contours which represent missing portions of the skull and which, therefore, can be no more than provisional reconstructions. The dentition in this specimen will first be described, and then the details of the skull itself.

Upper dentition (Pl. 2, fig. 4).—The central incisors are spatulate with a relatively thin biting edge. The lateral margins of the crown converge to an ill-defined basal tubercle behind, and from the tubercle a rounded central ridge extends down the posterior aspect of the crown. In the relative thinness of the spatulate crown, these incisors show a marked contrast with the massive construction of the central incisors in the modern large apes and, indeed, are strikingly similar in proportion to hominid teeth. The following measurements are the average of the two sides: width of biting edge 6·4 mm., maximum antero-posterior diameter at base 6·0 mm., and height of crown anteriorly 10·0 mm. The lateral incisors are much smaller than the central, and have a modified spatulate form. The inner margin of the crown is straight, but the outer margin is directed obliquely downwards and medially. The cingulum is well defined on the posterior aspect of the base, and is here thickened centrally to form a basal tubercle. The following are average measurements of the two sides—maximum width of crown 5·4 mm., and height of crown on its anterior aspect 7·0 mm.

The upper canines are stout teeth, but are markedly smaller, in absolute and relative size, than the upper canine of the holotype. It seems probable that this is a sexual difference. The average height of the crown (taken from the enamel base on the lateral aspect of the tooth) is 13·4 mm., and the diameters of the base of the crown 8·3 mm. and 9·0 mm. The crown is of pyramidal shape, terminating in a strong rounded point. The anterior aspect of the tooth is marked by a relatively deep vertical groove which above ends in a small recess beneath a rather strong anterior cingulum. The latter appears from the lateral aspect to form a distinct cuspule at the base of the tooth (see text-fig. 2), and is continued round on to the medial aspect of the base as the internal cingulum. The medial surface of the crown is very slightly concave, and faintly marked by vertical grooves. On the posterior margin is a long narrow facet made by contact with the anterior lower premolar. On the right side the canine is separated from the lateral incisor by a narrow diastema less than 2 mm. in width. On the left side, no such interval is present—evidently the result of a distortional compression on this side.

The upper premolars are not so delicately constructed as those of the holotype and, being well worn, do not show the cusp pattern so clearly. In both teeth the posterior cingulum is very distinct, and the central transverse ridge connecting the labial and lingual cusps is close to the anterior margin of the crown. In the less worn left anterior premolar the labial cusp projects well beyond the level of the lingual cusp, but even in the unworn condition it probably was not so prominent and sharp as in the holotype. Possibly, in relation to the smaller canine, this is also to be regarded as a sexual difference, the holotype representing a male individual and the skull a female. The dimensions of all the premolar and molar teeth in this specimen are given in Table 3.

The first upper molar is so closely similar to that of the holotype that no detailed description is necessary. It has been subjected to wear and the dentine is exposed at the apices of the main cusps. The hypocone is relatively well developed, and approximates in size to that of the protocone. The internal cingulum is strongly built, but has been partly obscured by attrition. The second molar is a little more regularly quadrate than the corresponding tooth of the holotype but is otherwise closely similar. The hypocone almost equals the protocone in size, and is broadly continuous with the internal cingulum. The posterior cingulum is but weakly developed. The last molar shows marked retrogressive features; it is much reduced in size, and the hypocone and metacone have disappeared to be replaced by irregular minor foldings of the enamel. The internal cingulum is elaborated by beading, and is continued round the posterior margin of the crown into a posterior cingulum. The crown of the last molar shows only a slight degree of wear, but attrition facets on the front part of the occlusal surface make it clear that it had come into use. It is certain, therefore, that this specimen belongs to a mature individual. The total length of the upper premolar-molar series is 36 mm.

The resemblance in size, proportions and cusp patterns between the upper dentition of the skull and that of the holotype of *P. africanus* is so close that the former may be assigned without hesitation to the same species.

Lower dentition (Pl. 2, fig. 5).—The lower incisors are chisel-shaped, relatively long and narrow, with straight biting edges. The average width of the biting edge on the two sides in the central incisors is 3·7 mm., and in the lateral 4·0 mm. The average height of the crown (measured on the anterior aspect of the tooth) is 9·2 mm. in the central incisors and 10·2 mm. in the lateral. In their antero-posterior thickness at the base the teeth are relatively more slender than in the large modern apes; this diameter measures 4·6 mm. in the central incisors and 6·0 mm. in the lateral.

The lower canines are relatively short and bluntly pointed, and are implanted almost vertically in the mandible. The anterior margin of the convex labial surface is continued below into a moderately developed internal cingulum. The lingual surface of the crown is slightly concave anteriorly. The maximum height of the crown (average of two sides), measured on the labial aspect, is 14·5 mm., the antero-posterior diameter of the base 6·2 mm., and the transverse diameter of the base 9·0 mm. There is no diastema in relation to the lower canines.

The anterior lower premolar is of sectorial form, compressed laterally and obliquely disposed in the axis of the tooth-row. The main cusp is strongly convex laterally, and slightly concave medially. These two surfaces are separated anteriorly by a crest which extends down obliquely from the apex to the anterior extremity of the internal cingulum. There is a small and rather inconspicuous talonid, the shallow basin of which extends up into a concavity on the posterior aspect of the main cusp. In the posterior premolars, the paired labial and lingual cusps of the trigonid region are both well developed, and are of approximately equal size. They are united by a low transverse crest in front of which is a small foveal depression. The talonid is well developed.

The first lower molar is a comparatively small, rectangular tooth. The protoconid, metaconid, and hypoconid are of approximately equal size, and the hypoconulid is median in position. The entoconid is relatively small so that there is a broad contact between the metaconid and hypoconid. A small and shallow anterior fovea is present close to the anterior margin of the crown. The external cingulum is distinct anteriorly, and also opposite the interval between the protoconid and hypoconid. The cusps have a clear-cut "crystalline" form, and there is an absence of secondary enamel folds. The second molar has a broader, rectangular crown. The hypoconulid is relatively small and displaced slightly lateral to the median axis of the tooth. A well-defined foveal depression is present postero-medially between the hypoconulid and the entoconid. The external cingulum is only to be distinguished anteriorly at the base of the metaconid. The third molar is elongated and narrows posteriorly to give the occlusal surface of the whole crown a sub-triangular shape. The hypoconulid forms the pointed posterior extremity of the tooth, and is aligned with the protoconid and hypoconid. The latter is somewhat reduced in size in comparison with the protoconid, and the entoconid is a very small and inconspicuous cusp. The whole length of the inner margin of the crown from the metaconid to the hypoconulid is irregularly wrinkled to form a series of small accessory cuspules. The external cingulum is well marked throughout its extent. The total length of the lower premolar-molar series is 43·5 mm.

The lower dentition in this skull, although slightly smaller in absolute dimensions, is almost identical in the proportions and cusp patterns of the premolars and molars with that of the specimen of a mandible C.M.H.102 described below, which was originally described and figured by MacInnes (1943). MacInnes tentatively assigned this mandible to Hopwood's genus *Xenopithecus*. We ourselves had also supposed that, in its relatively small size, the mandible C.M.H.102 could hardly be related to the maxilla of Hopwood's holotype of *P. africanus*. The discovery of the skull now makes it clear, however, that they belong to the same species, together with certain other specimens which had previously been allocated to the genus *Xenopithecus*.*

Description of the Skull

General features.—In lateral view, the outstanding characters of the skull are the pronounced prognathism, the inclination and receding disposition of the orbital aperture, the lack of a supra-orbital torus, and the small size of the brain-case (so far as this can be inferred from the incomplete calvaria). The outline of the occipital part of the skull indicated in text-fig. 2 is, of course, conjectural. However, some indication of its backward extent is provided by the direction of the curvature of the vertex of the preserved portion of the calvaria (which is even and apparently undistorted except near its posterior margin) and by a small part of the nuchal crest which is present close to the posterior broken edge of the brain-case. This section of the nuchal crest has been displaced slightly forwards in the specimen, and correction has been made for this in the reconstruction drawing. It seems hardly possible that the occipital region extended back further than it is shown in the reconstruction, though it may well have been rather more abbreviated. The exact position of the occipital condyles is also unknown for, although the condyles have been preserved attached to isolated fragments of the occipital bone, the absence of contacts makes it impossible to place them in their exact position in relation to the rest of the skull. The contour of the symphysis of the mandible shown in the reconstruction has been determined by correcting for the deformation which has resulted from a warping of this region and, as a further check, reference has been made to the undistorted symphysis in other specimens of the mandible of *P. africanus* (R.1948, 375, and S.9, 1938). Apart from these doubtful points, the reconstruction of the lateral view probably reproduces fairly closely the appearance of the undistorted skull from this aspect. The maxillo-facial and frontal region on the right side of the specimen show no clear evidence of post-mortem deformation. The possibility arises, however, that the degree of prognathism of the skull may be slightly exaggerated by warping, but any marked deformation in this respect seems to be precluded by the fact that it conforms with the proportions of the body and ascending ramus of the mandible which are well assured.

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* See footnote on p. 106.

From the reconstruction of the facial aspect of the skull (text-fig. 3), it appears that the facial skeleton was relatively broad, and the low and wide contour of the orbital aperture forms a striking feature. The proportions of the orbital margin can be determined with reasonable accuracy and, by taking measurements from the mid-line on the right side of the skull, it is possible to get a close approximation to the inter-orbital width and also the total width of the face. The mid-line itself (as may be seen by reference to the photograph in Pl. 1, fig. 2) has been twisted by the warping of the skull as a whole, and it has thus been necessary to make corrections for this in the reconstruction. A further check has been obtained by reference to the undistorted mandible of *P. africanus* (1948, 375) shown in Pl. 3, fig. 10. This mandible is a little smaller in general proportions than that of the skull, but it provides an indication that the total width of the latter could hardly have been less than that shown in the reconstruction.

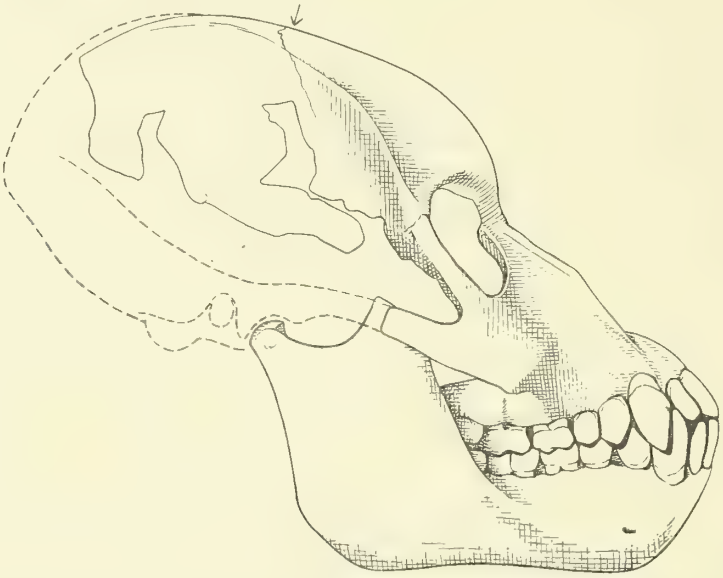

Fig. 2. Graphic reconstruction of the lateral view of the skull of *P. africanus* (R.1948, 50). The position of the bregma is indicated by an arrow. × $\frac{2}{3}$.

A reconstruction of the vertex of the skull emphasizes the relative breadth of the calvaria, and also shows that (associated with the backward position of the orbital apertures relative to the brain-case) the post-orbital constriction is much less marked than it is in the adult skulls of the modern anthropoid apes.

Orbital region.—The right orbital aperture is complete except for a small fragment about 6 mm. long at the centre of the medial margin. It also appears to be almost entirely undistorted. The frontal process of the maxilla has been fractured, but the fragments fit together accurately and if there is any displacement here it must be very slight. The maximum width of the orbital aperture (in the long axis) is 30 mm., and its maximum height (at right angles to the long axis) is 24 mm. The oblong shape of the aperture, combined with a slightly oblique disposition of its long axis, gives it an appearance very different from that seen in the modern anthropoid apes (in which the orbits are characterized not only by their relatively large size but also by their somewhat circular contour). In its general appearance, indeed, the orbit has a rather curiously human resemblance, an impression which is no doubt enhanced by the relative breadth of the inter-orbital space and the modelling of the supra-orbital region. The minimum inter-orbital distance (i.e. between the medial margins of the orbit) is estimated to be 14 mm.

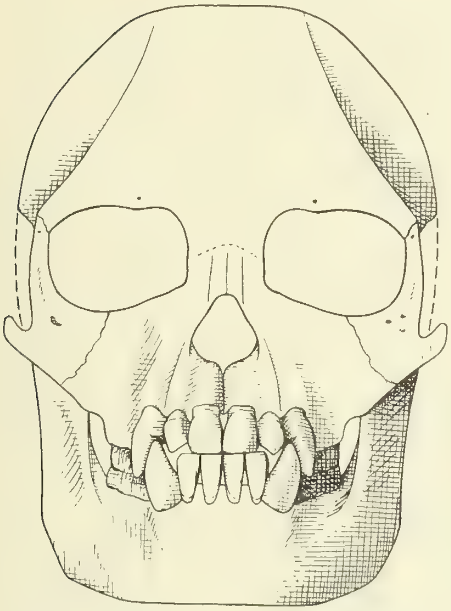

FIG. 3. Graphic reconstruction of the facial aspect of the skull of *P. africanus*. × ⅔.

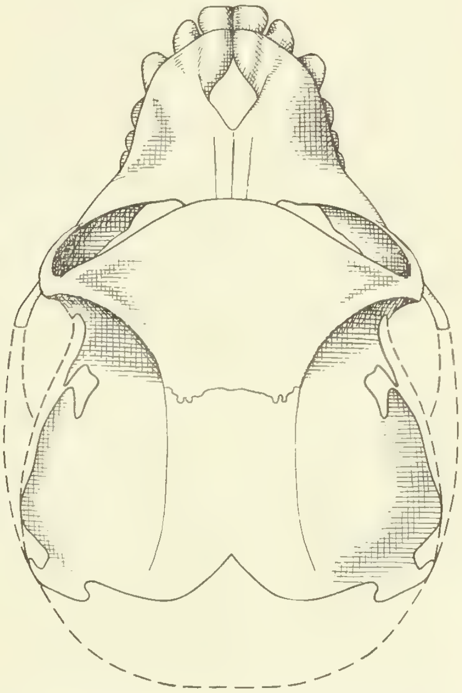

FIG. 4. Graphic reconstruction of the skull of *P. africanus* from above. × ⅔.

At the medial margin of the orbit, the anterior half of the lacrimal fossa is preserved. The lateral margin of the orbit is sharply defined and, from the side view, is seen to be drawn back a little behind the level of the medial margin. Above, it forms a rather abrupt angle with the superior margin (at the fronto-zygomatic suture) while below it curves gradually into continuity with the inferior margin. A narrow strip of the orbital surface of the zygomatic bone is retained, and shows a relatively large, single, zygomatico-orbital foramen (for the zygomatic nerve). The foramen is situated close to the orbital aperture—about 4 mm. from the lower end of the lateral margin. In its forward position and its relative size it corresponds with the condition commonly seen in the chimpanzee and orang. The inferior margin of the orbit slopes upwards in a medial direction (so that the orbital height is distinctly greater in its lateral half), and it forms a sharp border throughout its extent. The position of the upper end of the zygomatico-maxillary suture is only faintly indicated; it is shown in text-fig. 3. The superior orbital margin is formed by a sharp, thin, overhanging border in its lateral two-thirds and by an evenly rounded surface in its medial third. At the junction of these two parts is a shallow supra-orbital notch, and just above this a small foramen. The latter is apparently not a true supra-orbital foramen, for it has no obvious counterpart on the small area of the orbital roof which is still preserved; it is probably the small diploic foramen commonly to be found in the immediate vicinity of the supra-orbital notch.

The supra-orbital and frontal regions.—The supra-orbital region shows the complete absence of a torus, and even of a narrow raised supra-orbital rim such as is found in the adult orang. Medially, the position of the glabella is occupied by an even, rounded convexity which above shows no demarcation from the convexity of the frontal bone as a whole; below, it curves into a shallow nasionic depression. Laterally, the glabellar convexity is gradually replaced by a shallow concavity situated just above the lateral two-thirds of the superior orbital margin and extending on to the zygomatic process of the frontal. This process is a slender triangular plate of bone, narrowing to a width of 7 mm. where it articulates with the zygomatic bone. The modelling of the supra-orbital region, formed by the smooth glabellar prominence medially and the shallow concavity laterally, is quite unlike that seen in the modern anthropoid apes. As already noted, the fronto-zygomatic suture is placed at the junction of the superior and lateral margins of the orbit. Herein it makes an interesting contrast with the modern Ponginae, for in the latter (and particularly in the orang) the zygomatic process of the frontal extends downwards for a variable extent so that the suture tends to be displaced well on to the lateral margin of the orbital aperture.

From the region of the glabella the convex surface of the frontal bone slopes evenly upwards and backwards. Its posterior extent, and the position of the bregma, can be determined by the fact that the coronal suture is still patent in its upper part. The direct distance between the nasion and the bregma is approximately 57 mm. The posterior border of the frontal bone on the vertex of the skull (between the temporal crests) is disposed transversely and is not prolonged backwards to a receding angle in the mid-line as is characteristically the case in the gibbon. The position of the bregma is indicated in text-fig. 2 by an arrow. From the bregma, the coronal suture extends downwards and a little forwards, but its course can only be followed with certainty for a short distance. No sutures demarcating the greater wing of the sphenoid can be detected. The posterior margin of the zygomatic process of the frontal is continued upwards and backwards into the temporal line which limits the temporal fossa. On the right side the temporal line is present throughout its extent as far back as the posterior parietal region. On the left it can be traced in part of its course, but it has here been much displaced by fractures. Except anteriorly it is not strongly marked, and at the vertex of the skull it does not approach more closely to the mid-line than 13 mm. In association with the recession of the lateral margin of the orbit and the absence of a protruding supra-orbital torus, the post-orbital constriction in the skull, as already noted, is not very marked. A fracture line in the mid-frontal region has exposed the frontal air sinus; it extends upwards for a distance of at least 30 mm. above the nasion. On the other hand, its backward extension into the orbital roof is limited to not more than 8 mm. from the superior orbital margin.

Parietal region.—The greater part of the right parietal bone is preserved, though fractured and somewhat distorted posteriorly. Such fragments as remain on the left side are grossly distorted. Close to the posterior margin of the most posterior fragment of the right parietal region is a short length (17 mm.) of the nuchal crest. Although this fragment has been displaced slightly forwards, it provides a useful indication of the position of the nuchal crest in the intact skull. The skull roof is remarkably thin in the frontal and parietal regions, being in some places (e.g. over the convolutional convexities) near the vertex only 2–3 mm. thick, and in the lower part of the parietal bone about 1·5 mm.

Maxillary region.—On the right side the maxilla is complete except for a small piece missing in the position of the infra-orbital foramen. The details of the latter are thus not available. The body of the maxilla shows a pronounced concavity on its lateral surface (canine fossa) behind the prominence formed by the root of the canine. The lower border of the root of the zygomatic process is situated about 6 mm. above the alveolar border, at the level of the interval between the first and second molars. Immediately lateral to its origin from the body of the maxilla is a small tubercle marking the attachment of the anterior border of the masseter muscle. The course of the zygomatico-maxillary suture is somewhat obscured, but its general trend can be followed. The maxillo-premaxillary suture is distinct on both sides throughout the greater part of its extent. Below it can be traced to the anterior margin of the socket for the canine, and above it runs alongside the lateral margin of the nasal aperture at a distance from the latter of about 2 mm. On neither side can the upper extremity of the suture be defined, but two isolated maxillary fragments, to be described later (C.M.H.101 and 693), show that in *P. africanus* it meets the lateral margin of the nasal aperture at about the middle of its extent. The premaxillary element is relatively small as compared with that of the modern anthropoid apes.

Nasal bones.—The greater part of the nasal bone on each side is preserved and the naso-maxillary sutures are quite clearly defined. The lower margins of the bones are missing, and it is difficult to define the precise position of the fronto-nasal suture. Some traces of the latter, however, make it reasonably certain that it was disposed as shown in text-fig. 3. The total breadth of the two nasal bones together is 7 mm. near their lower margins, and about 6 mm. near the fronto-nasal sutures. They are each slightly concave from side to side, so that a low median elevation is produced along their line of contact at the inter-nasal suture. In the shape of the nasal bones, *P. africanus* approaches the gibbon much more closely than it does the modern large apes.

Nasal aperture.—The margins of the nasal aperture are well defined below, and on the left side much of the lateral margin is preserved. The upper margin is missing, but by reference to the inclination of the preserved parts of the lateral margins it can be reconstructed with some confidence. The nasal aperture is estimated to be 14 mm.

in width, and about 23 mm. in height; its lower extremity narrows by the folding together of the inner convex margins of the premaxillae to form a seam-like groove extending down the mid-line between the roots of the central incisors. In this feature the nasal aperture shows an interesting resemblance to the cercopithecoid monkeys and contrasts rather strongly with the broad gutter-like base of the nasal aperture, sloping gradually on to the convexity of the premaxilla, in the modern large apes. In the immature chimpanzee, however, a condition similar to that in *P. africanus* may be present. The pointed lower extremity of the nasal aperture extends down to a distance of not more than 11 mm. from the alveolar margin in the mid-line.

Zygomatic region.—The right zygomatic bone is preserved in its entirety; only part of the left remains. The facial surface of the main part of the bone is smooth and looks forwards and slightly outwards. The zygomatico-facial foramen appears to be single on the right side (it is partly obscured by matrix), but on the left side it is represented by three separate openings. The frontal process is slender, measuring in width a little over 7 mm. at its base and about 5 mm. near its upper extremity. Its facial surface is marked by a longitudinal groove such as is not uncommonly seen in *Hylobates*. The groove leads down to one of the zygomatico-facial foramina and presumably lodges a branch of the nerve which emerges here. At the upper extremity of the frontal process, close to the zygomatico-frontal suture, is a small (? vascular) foramen on either side. The temporal process of the zygomatic bone extends backwards and a little upwards. In width it measures about 6 mm. near its posterior end. The zygomatico-temporal suture cannot be certainly defined. Only a small part of the orbital surface of the zygomatic bone is preserved.

Palate.—The palate is complete except for the posterior margin, but it is distorted by crushing. Hence, only approximate measurements can be made. The width of the palate between the inner margins of the canine sockets is estimated at about 20 mm., and between the first molars probably about 24 mm. Thus, the dimensions are closely similar to those estimated for the holotype of *P. africanus*. The total length of the palate from the level of the posterior margins of the central incisor sockets to the transverse level of the posterior margins of the last molar crowns is approximately 45 mm. Because of distortion, it is not possible to determine with accuracy the degree of divergence of the premolar-molar series. There are no significant features of the surface of the palate which merit description. The incisive fossa is ill-defined and there is no certain trace of the maxillo-premaxillary suture.

Occipital bone.—Two isolated portions of the occipital bone are available for study. Unfortunately, neither of them can be placed accurately in relation to the rest of the skull because there are no contacts. One fragment consists of the right condyle, and the right border and anterior half of the basi-occipital. The condyle measures 12·6 mm. in its long axis, and its maximum width is 7·4 mm. It is rather acutely curved at the junction of its middle and posterior thirds. The hypoglossal canal is single and appears to be disproportionately small, with a maximum diameter at its inner end of 1·5 mm., and at its outer end of 2·0 mm. The width of the anterior end of the basi-occipital element is approximately 13 mm. On its lower surface the front end of a low median ridge is preserved, and its upper surface is evenly concave from side to side. The other occipital fragment comprises a considerable part of the post-occipital element and the posterior margin of the foramen magnum, and also the left condyle (which is crushed and distorted). Behind the condyle is a well-defined posterior condylar fossa, but no posterior condylar foramen. The posterior margin of the foramen magnum is thin and sharp. By placing the two fragments of occipital bone in relation to each other, it is possible to get an approximate estimate of the dimensions of the foramen magnum—the antero-posterior diameter is about 20 mm., and the transverse about 17 mm. The outer surface of the post-occipital element shows a median elevation (corresponding to the vermiform fossa), and on either side of this the surface is broadly concave. The bone is extremely thin in the region of the vermiform fossa—in some places less than 1 mm. The endocranial aspect of the post-occipital shows a broad and rather deep vermiform fossa, with a maximum width of approximately 9 mm. At the upper extremity of the fossa are seen the diverging grooves for the lateral venous sinuses, the lower border at the point of divergence being 19 mm. above and behind the posterior margin of the foramen magnum. The venous grooves are of equal size and measure in width near their origin about 4 mm. The broken edge of this post-occipital fragment is immediately above the bifurcation of the groove for the superior sagittal sinus, and here the thickness of the bone increases to 4 mm.

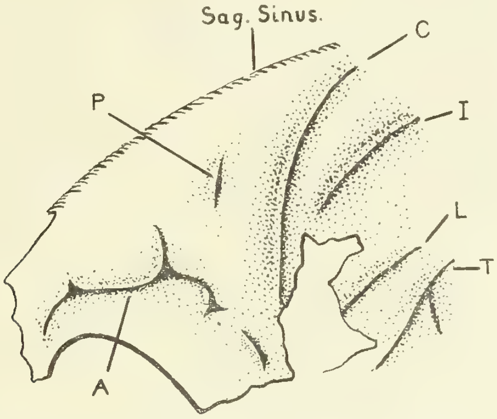

FIG. 5. A drawing made to scale showing the sulcal markings on the endocranial aspect of the frontal and anterior parietal regions of the right side of the skull of *P. africanus*. Natural size. The following are the provisional identifications of the sulcal impressions. A. Arcuate sulcus, C. Central sulcus, I. Intra-parietal sulcus, L. Lateral sulcus, P. Superior precentral sulcus, T. Superior temporal sulcus.

Endocranial aspect of the skull.—On the endocranial surface of the frontal and parietal regions, impressions of sulci and the superior sagittal venous sinus are to be seen. The groove for the sinus is distinct in the mid-line of the frontal region, and here it has a maximum width of 3 mm. No definite markings of arachnoid granulations are present. The sulcal impressions are strongly represented, but in the absence of a more complete specimen their identification must be provisional. In text-fig. 5 a scale drawing is shown of the sulcal impressions as they are seen when viewed somewhat from below and behind. A single, long, and uninterrupted sulcal ridge (C) extends downwards and forwards from the vertex, and can be traced in continuity for over 30 mm. Above, it inclines backwards and reaches a point about 6 mm. from the mid-line and 10 mm. behind the level of the bregma. Below, it ends at a fractured margin of the skull in the region of the antero-inferior angle of the parietal bone. There can be little doubt that this ridge represents the sulcus centralis. It corresponds in position and extent with the impression for the s. centralis which is often evident in the skull of *Hylobates*, and its uninterrupted and unbranched course seems to preclude any other interpretation. At a distance of 10 mm. in front of the middle of the central sulcus impression is a localized and well-defined sulcal impression (P) which probably represents the superior precentral sulcus. It runs a very short course downwards and forwards, and its upper limit is situated 10 mm. from the mid-line. More anteriorly and below, a strongly marked sulcal ridge (A) arches forwards, above the broken margin of the orbital roof, towards the region of the frontal pole. Its position and course are shown in the diagram in text-fig. 5, from which it will be seen that a short vertical ramus is given off at the junction of its posterior and middle thirds. The sulcus represented by this impression is here identified as the arcuate sulcus. Below and behind its posterior extremity is another small sulcal impression, the identification of which is less certain. Behind the middle part of the sulcus centralis ridge, and converging to a point about 6 mm. from the latter, is seen the impression of the anterior end of a sulcus (I) extending forwards and downwards in the parietal region. In its disposition it corresponds closely to the intraparietal sulcus of the cercopithecoid brain. Its posterior extent is not clearly definable in the fossil skull. Finally, there are short segments of two sulcal impressions in the lower parietal region (L, T) which may represent parts of the lateral and superior temporal sulci.

The main interest of these sulcal impressions depends on the identification of the position of the sulcus centralis, for, if this identification is valid, it indicates that the frontal lobe of the brain in *P. africanus* was relatively small, and that its convolutional pattern was very simple and of a cercopithecoid rather than a hominoid type. The existence of sulci in the frontal lobe of the brain, other than those shown in text-fig. 5, cannot be entirely denied, of course, but the clearness of the definition of the sulcal impressions which have been described suggest that, if other sulci were present, they must have been small and very shallow. The cercopithecoid appearance of the sulcal pattern is further enhanced by the position and direction of the impression which is believed to represent the sulcus intraparietalis, and particularly in its oblique approach to the lower part of the sulcus centralis impression. The size of the frontal lobe as a whole cannot be computed from the fossil skull; absence of the orbital roof (except for a strip adjacent to the margin of the orbital aperture) precludes a definition of the lower border and the contour of the rostrum.

Among the small fragments of the skull which it is not possible to fit into position are pieces of the two petrous bones, each containing the internal auditory meatus and the subarcuate fossa. The former can be accurately defined on the right side and measures 3·4 mm. in its maximum diameter. At a distance of 3 mm. from its lateral border is the opening of the subarcuate fossa which accommodates the petrosal lobule of the cerebellum. This fossa has a clear-cut oval aperture measuring 3·5 mm. in vertical diameter, and has a depth of just over 4 mm. The lower and posterior part of the margin of the aperture shows the characteristic fine ribbing which is commonly present also in the subarcuate fossa of *Hylobates* and the cercopithecoid monkeys. Taken in conjunction with the broad vermiform fossa in the occipital bone, the relatively large subarcuate fossa indicates a cerebellum of somewhat primitive type.

Mandible (Pl. 2, fig. 6 and text-fig. 10B). The mandible attached to the fossil skull is practically complete, and it is well-preserved except for the effects of distortion which affect the left side and the incisor region. The main dimensions are as follows:

Total length of premolar-molar series	43·5 mm.
Length of symphysis anteriorly in mid-line	28 ,,
Maximum antero-posterior thickness of symphysis	12 ,,
Height of body opposite M $\overline{1}$	20 ,,
Maximum width of body at level of M $\overline{1}$	10 ,,
Height of vertical ramus to middle of sigmoid notch	46 ,,
Width of middle of vertical ramus	33 ,,
Average width of condyles	12·6 ,,
Maximum antero-posterior thickness of condyles	4·5 ,,
Maximum width of sigmoid notch	18·5 ,,

The upper part of the symphysial region has evidently been displaced a little forwards as the result of warping. Correction for this has been made in the diagram shown in text-fig. 10B, the reconstruction being checked by reference to other specimens of the symphysial region of *P. africanus*, and particularly to the undistorted mandible in specimen R.1948, 375 (*vide infra*). The anterior surface of the symphysis in its normal condition slopes evenly downwards and a little backwards, and terminates at its lower border in a small median tubercle for the attachment of the mylohyoid raphe. The posterior aspect of the symphysis slopes downwards and backwards to a small, shallow genial fossa situated 7 mm. above the lower border. There is no simian shelf.

The body of the mandible narrows from above downwards to a very slight degree towards the level of the last molar. It has a thick rounded lower border, and the upper part of its lateral surface shows a shallow concavity below the premolars and first molar. The mental foramen, which is single, is placed vertically below the anterior premolar, nearer the lower than the upper border of the body of the mandible.

Whereas the body of the mandible is stoutly constructed, the ascending ramus is thin. The anterior border extends down to overlap the posterior two-thirds of the last molar. Above, it slopes upwards and a little backwards to the coronoid process. The latter recurves to a well-defined point, and the sigmoid notch is relatively deep.

The condyles are well preserved. They appear to show no unusual feature except that the long axis is disposed rather more obliquely medially and backwards than is commonly seen in the modern (adult) anthropoid apes. However, a detailed comparative study might show significant differences in the curvature of the articular surface. The total bicondylar width (between the lateral extremities of the condyles) is difficult to determine because of the distortion of the mandible as a whole, but by reference to the median axis of the symphysis it is estimated to be approximately 82 mm.

The lateral surface of the ascending ramus shows a pronounced concavity above and in front, otherwise it is smooth and flat. The angle of the jaw is only slightly roughened by muscular attachments. On the inner aspect of the ramus a smooth, rounded ridge extends downwards and forwards from the condylar process towards the posterior end of the alveolar border. The mandibular (inferior dental) foramen is situated in the centre of the ascending ramus, and a shallow groove for the mylohyoid nerve can be seen running obliquely downwards and forwards just below the foramen. Slight irregularities on the inner surface of the angle mark the insertion of the medial pterygoid muscle.

Other Specimens of *Proconsul africanus*

Besides the holotype of *P. africanus* and the skull, a number of teeth and jaw fragments referable to the same species have been found in the Miocene deposits of East Africa.

*C.M.H.*102.—(Found on Rusinga Island at the site where the 1942 mandible was discovered.) Part of a lower jaw, with the posterior premolar and the three molars of the left side almost perfectly preserved (Pl. 3, figs. 8, 9). As already mentioned, it was provisionally allocated by MacInnes to *Xenopithecus koruensis*, mainly on account of its size (MacInnes, 1943, pl. 23, figs. 7, 7a).

The specimen includes the symphysial region, and part of the body of the left side, the crowns of P $\overline{4}$–M $\overline{3}$ on the left side, the roots of P $\overline{3}$ of both sides, and the sockets of the two canines. The sockets of the incisor teeth are obscured by matrix. The total length of the premolar-molar series is estimated to have been 43 mm. This compares with 43·5 mm. in the skull (R.1948, 50). The width between the inner margins of the canine sockets is about 12 mm. and that between the inner margins of the first molars about 18–20 mm. (measurements which are approximately similar to those in the skull).

The only other features which merit attention here are (1) the symphysis shows on its posterior aspect near the lower border a well-defined median genial pit; (2) although the lower border of the symphysis is defective, it is certain that the simian shelf was absent; (3) the whole mandible was relatively robust, the antero-posterior thickness of the symphysis at its maximum being 14·0 mm., while the thickness of the body at the level of the second molar is at least 12·5 mm.; (4) the mental foramen is situated at the level of the posterior half of P $\overline{3}$.

The details of the lower teeth which are preserved in the mandible are as follows. In all their characters they are remarkably similar to those of the skull (R.1948, 50).

P $\overline{4}$.—The two main cusps are sub-equal and moderately worn. They are united by a transverse crest, and the latter is separated in front from the anterior cingulum by a foveal depression. The talonid is relatively extensive and hollowed out into a broad basin. The crest forming the posterior boundary of this basin is continued laterally for a short distance on to the base of the labial cusp, giving here an indication of a postero-external cingulum. There is also a very faint trace of an antero-external cingulum.

M $\overline{1}$.—As in all species of the genus *Proconsul*, this tooth is relatively small in proportion to the other molars. The crown is of a somewhat rectangular shape (slightly broader in its posterior moiety), and, as in all the molars, the cusps are sharply "crystalline" in appearance, with flattened polyhedral surfaces almost devoid of secondary wrinklings. There is a small anterior fovea in front of a low transverse ridge connecting the protoconid and metaconid. The hypoconid is relatively large and makes a broad contact with the metaconid. The entoconid is thus widely separated in the centre of the crown from the protoconid. A relatively small but well-defined hypoconulid is present. At the postero-medial margin of the crown is a small posterior fovea, somewhat obscured by attrition. Rather distinct traces of an external cingulum are present at the centre of the lateral margin of the crown (opposite the interval between the protoconid and hypoconid) and at the postero-lateral angle. A faint remnant is also visible at the antero-lateral angle.

M $\overline{2}$.—Except for its larger size, this tooth shows much the same features as the first molar. The antero-external cingulum is more pronounced, the entoconid and hypoconulid are relatively larger, and the crown has a lower breadth index. The crown is rectangular in shape, the anterior and posterior moieties being of equal width.

M $\overline{3}$.—A conspicuously elongated tooth, broadest in the trigonid portion, and tapering to its posterior margin. The lateral surface of the crown is partly missing, but what remains shows that the external cingulum was quite well developed. The protoconid and metaconid are of approximately equal size, the entoconid is unusually small, while the hypoconulid is enlarged to produce a prominent heel and is marked on its central aspect by a number of secondary enamel wrinkles.

R.1948, 375 (Pl. 3, fig. 10).—A much weathered mandible which is almost complete except for the ascending rami. It was recovered from deposits on the ridge linking Lunene with Sienga on Rusinga Island. In spite of its poor state of preservation, it provides very useful information regarding the symphysial region and the degree of divergence of the horizontal rami, for there is no evidence of distortion by pressure or warping. In its general size and proportions the mandible compares very closely with that belonging to the skull of *P. africanus* (R.1948, 50), but it is slightly smaller. The incisors, canines, and right anterior premolar are represented only by their sockets, and the two premolars of the left side by their roots. The other teeth, including the third molars, which are fully erupted and show exposure of the dentine by attrition, are very badly weathered, most of the enamel having been eroded or flaked off. The total length of the mid-line of the symphysis on its anterior aspect is approximately 26 mm. At its lower border is a small backwardly directed spine for the attachment of the mylohyoid raphe. The posterior surface of the symphysis slopes downwards and backwards and ends in a shallow genial pit, the upper margin of which is 8 mm. above the lower border of the symphysis. There is no simian shelf. The maximum thickness of the symphysis (measured at right angles to the anterior surface) is 12·5 mm. The body of the mandible shows a well-marked shallow concavity in the upper half of its lateral surface, extending back from the level of the anterior premolar to the posterior border of the first molar. The height of the body opposite the anterior premolar, and also opposite the middle of the second molar, is about 20 mm. The maximum thickness of the body opposite the middle of the second molar is about 12 mm. The maximum width of the whole mandible at the level of the posterior margins of the last molars is 59 mm. The mental foramen, which is single, is situated at the level of the anterior premolar, slightly nearer the lower than the alveolar border. On the right side the lower end of the anterior border of the ascending ramus is present, extending downwards and forwards as a strong rounded ridge on to the body of the mandible. From the lateral view, this border obscures the posterior third of the last molar tooth. The total width of the incisor sockets is 14 mm. The socket for the canine measures approximately 7 mm. in antero-posterior diameter; its transverse diameter cannot be measured, owing to the breaking away of the lateral margin.

As already mentioned, the crowns of the teeth which have been preserved are very severely weathered so that very few details of the cusp pattern can be defined. At first sight, the molars appear to be considerably narrower than those of specimens R.1948, 50, and C.M.H.102. A close examination, however, makes it almost certain that this appearance is illusory, due to flaking and erosion of the enamel. The total length of the premolar-molar series is estimated to be 41 mm. So far as can be ascertained, the cusp pattern of the molars is similar to the specimens of *P. africanus* already described. As may be seen by reference to the photograph (Pl. 3, fig. 10), the premolar-molar series converge anteriorly to a rather marked degree. The angle of convergence formed by the central axes of the tooth rows is 25°. According to the data recorded by Werth (1919), this corresponds to the degree of convergence in *Pliopithecus*, but exceeds that of *Hylobates* (20°–21°). The transverse width between the inner margins of the roots of the anterior premolar is 18·5 mm., and between the inner margins of the posterior roots of M $\overline{3}$ approximately 34 mm.

S.21 (MacInnes, 1943, pl. 23, fig. 11).—This mandibular fragment from Songhor contains the relatively unworn, but somewhat weathered, posterior premolar and the first and second molars. These are very similar in the details of cusp pattern to the corresponding teeth in C.M.H.102, but they are somewhat smaller and also narrower. The entoconid and hypoconulid are relatively small in M $\overline{1}$.

1230, 1947 (*Kathwanga*).—A fragment of mandible containing the much worn posterior premolar and first molar, and the roots of the anterior premolar. P $\overline{4}$ and M $\overline{1}$ agree closely in size and proportions with the corresponding teeth in C.M.H.102, except that the premolar is relatively a little more massive. A portion of the root of the canine is still embedded in the alveolus, from which it can be estimated that the minimum diameter of the root at its upper end was approximately 5·5 mm. The roots of the premolars are exposed in this specimen, and it is apparent that in both teeth there are two buccal roots and one lingual.

S.9, 1938 (MacInnes, 1943, pl. 23, fig. 8).—The symphysial region of the mandible containing, in good preservation, the sockets for all the incisor and canine teeth, and also the roots of the premolars of both sides and of the right first molar (text-fig. 6). The dimensions of the sockets of the front teeth at the level of the alveolar border are as follows:

	tr.	*a.p.*
I $\overline{1}$	2·4 mm.	4·2 mm.
I $\overline{2}$	2·6 ,,	5·3 ,,
C	5·4 ,,	8·2 ,,

The minimum distance between the medial margins of the canine sockets is 13·2 mm., while the maximum width of the mandible at the lateral margins is approximately 24 mm. The symphysis is strongly constructed. Its posterior aspect shows an even slope downwards and backwards from the incisor region as far as the upper margin of the genial fossa. The latter is relatively large and centrally situated. The lower margin of the symphysis in the mid-line shows a small tubercle—presumably for the attachment of the mylohyoid raphe. The length of the anterior surface of the symphysis in the mid-line is 27 mm. There is no simian shelf. In its general dimensions, this symphysial fragment corresponds closely with specimens R.1948, 50 and C.M.H.102. The vertical height of the body of the mandible from the alveolar margin at the level of P $\overline{4}$ is 22 mm.

*C.M.H.*129 (*Rs.*30).—A fragment of the left side of the mandible with the second and third molars, both considerably worn and badly weathered. Very little can be made out of the details of the cusp pattern. By reference to their size and proportions, however, these may be assigned with reasonable certainty to *P. africanus*. The vertical height of the body of the mandible from the alveolar margin at the level of M $\overline{2}$ in this specimen is 20·5 mm., and its maximum thickness at the same level is 12 mm.

599 (*R.*106), 1947.—The symphysial region and anterior part of the left side of the body of a mandible, containing the somewhat eroded sockets of all the incisors, and the roots of the canine, premolars and first molar of the left side. The identification of this fragment is based on its general size and the dimensions of the roots of the teeth. It harmonizes very closely with the mandibular specimens of *P. africanus* described above, the main difference being a rather less massive symphysis, and the absence of a well-defined genial fossa. The dimensions of the root of the canine at the level of the alveolar margin are approximately 8·5 mm. and 6·0 mm. The vertical height of the body of the mandible from the alveolar margin at the level of P $\overline{4}$ is 22 mm., and the maximum thickness of the body at the level of M $\overline{1}$ is 11 mm. There is a well-marked, single, mental foramen at the level of the interval between P $\overline{3}$ and P $\overline{4}$.

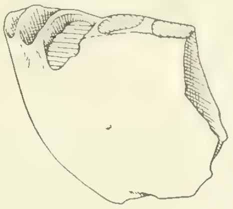

FIG. 6. Symphysial region of mandible of *P. africanus* (S.9, 1938) viewed from the left side. Natural size.

*C.M.H.*8 (*R.*3).—A portion of the right side of the body of a mandible with the badly damaged crowns of the first and second molars, a broken portion of the posterior premolar, and the weathered socket of the last molar. The enamel has been almost entirely flaked off the teeth. The height of the mandible at the level of M $\overline{1}$ is 22 mm., and its maximum thickness at the same level 9 mm. The mental foramen is situated at the level of the anterior margin of the posterior premolar, a little below the centre of the body. This specimen is not part of an immature mandible of a larger species; a radiograph shows no unerupted teeth. The third molar, however, may not have completed its eruption.

F.3104 (*S*).—A small fragment of the left side of the body of a mandible with the roots of the three molar teeth. The identification of this specimen is doubtful; it is here assigned to *P. africanus* on account of the size of the molar teeth as indicated by their roots and the robust proportions of the mandible. The latter, however, is rather small; the vertical height of the body at the level of M $\overline{2}$ is not more than 17 mm.

*C.M.H.*101 (*Rs*.35).—Part of a much weathered left maxilla which in size corresponds very closely with that of specimen R.1948, 50. It includes a small portion of the margin of the nasal aperture, the lateral wall of the socket for the first incisor (and the upper end of the root of this tooth), the root of the second incisor, the broken crown of the canine, and the extremely weathered crowns of the premolars and the first molar. Because of the weathering of the last three teeth, no details of the cusp pattern are discernible and accurate measurements are not obtainable.

The lower margin of the nasal aperture is rounded, and extends down to a distance of 9·0 mm. above the alveolar margin at the level of the lateral margin of the median incisor. The premaxillary suture is quite clearly seen—it extends up almost vertically on the facial aspect of the bone to reach the margin of the nasal aperture at a distance of 17 mm. above the alveolar margin, and approximately 7·0 mm. above the lower margin of the nasal aperture, on a level with the anterior margin of the canine. The root of the lateral incisor at the alveolar margin measures 5·0 mm. by 3·3 mm.; it is separated from the canine by a narrow diastema of about 2 mm. The cross-sectional dimensions of the weathered root of the canine at the alveolar level are 8·5 by 6·5 mm., as compared with 9 and 8·3 mm. in the skull of *P. africanus*. The root is implanted almost vertically in the maxilla and ascends to a distance of about 19·0 mm. above the alveolar margin. The base of the zygomatic process starts to rise at the level of the anterior border of the first molar and close to the alveolar margin. The width of the palate between the inner margins of the canines is estimated, rather uncertainly, from this fragment to have been about 18 mm. The allocation of this specimen to *P. africanus*, it will be noted, rests on its general proportions.

693, 1947 (*R*.106).—This reference number comprises a portion of a right maxilla and premaxilla containing the roots of the two incisors, canine and anterior premolar, a portion of another right maxilla containing the roots of the two premolars and first molar, and an isolated right lower lateral incisor. All these specimens have been exposed to weathering. The maxillary fragments conform very closely indeed in size and proportions with that of the previous specimen (C.M.H.101). The premaxillary suture is visible in its facial and palatal course and extends up almost vertically to reach the lateral margin of the nasal aperture about 10 mm. above the lower margin of the latter, and about 18 mm. above the alveolar margin. The lower margin of the nasal aperture is situated about 10 mm. above the level of the alveolar margin at the lateral border of the median incisor tooth.

The width of the palate between the inner margins of the canines can be estimated with reasonable accuracy in the more anterior fragment of maxilla, for the position of the mid-line is indicated by the inner margin of the medial incisor; it is about 14·0 mm. The more posterior fragment includes a portion of the palate, the median line of which is approximately indicated by a slight ridge on its upper surface. From this the width of the palate between the inner margins of the first molars is estimated at about 20·0 mm.

The root of the median upper incisor tooth is stout, having (near the alveolar margin) a transverse width of 5·0 mm., and an antero-posterior diameter of 4·4 mm. The root is set obliquely in the premaxilla, at an angle of about 45°. The corresponding diameters of the root of the lateral incisor are 4·0 mm. and 4·2 mm. This tooth is separated from the canine by a diastema of 2·8 mm. The root of the canine at the alveolar margin measures 7·8 mm. in antero-posterior diameter and 6·0 mm. in transverse. The roots of the premolars and first molar are too fragmentary and weathered to permit of measurements. As with specimen C.M.H.101, the identification of these maxillary fragments is based on their general proportions.

The isolated lower incisor tooth associated with the above specimens is weathered and broken. Its root, markedly compressed from side to side, conforms in size and proportions closely with the lower incisor teeth in the skull (R.1948, 50). With these fragments of maxillae and the isolated incisor were also found the articular head of a femur (diameter 14 mm.) and a middle phalanx (length 18 mm.). There must remain some doubt whether these limb-bone fragments belong to the same creature as that represented by the maxillary specimens. In any case, however, they do not by themselves contribute information of much value, apart from their actual size.

S.15, 1947 (Pl. 3, fig. 11).—A maxillary fragment with a portion of the palate and the base of the zygomatic process containing the posterior premolar and the first molar, in an excellent state of preservation, and only slightly faceted by wear. The first molar accords with that of *P. africanus* in its general cusp pattern, but it is a smaller and much narrower tooth. The posterior premolar also has a much lower breadth index. The molar shows the same degree of development of the cingula (particularly the internal cingulum), and the relative size of the cusps is also in agreement. The fragment clearly belongs to an animal much smaller than those represented by the other specimens of *P. africanus*. This is shown not only by the size of the teeth, but also of the maxilla. The median suture of the palate is exposed at the medial margin of the palatal process, from which the total width of the palate between the inner margins of the first molar teeth can be estimated at not more than 15·0 mm., as compared with about 24 mm. in the holotype and in the skull (R.1948, 50). The specimen may represent an animal which is not quite mature. A pressure facet on the posterior surface of the first molar indicates that the second molar had fully erupted. On the other hand, the third molar may not have completed its eruption. Even so, however, the narrowness of the palate is a striking feature. In view of these differences (and certain differences in the details of the cusp pattern of the molar) there must remain some doubt of the identification of this specimen, and subsequent discoveries may show that it represents a distinct species. The details of the posterior premolar and first molar are as follows:

P $\underline{4}$.—The labial and lingual cusps are of approximately equal size, the former projecting to a slightly lower level. The cusps are separated by a broad valley crossed from side to side by exceedingly fine enamel ridges. From the summit of the lingual cusp a strong ridge extends downwards and laterally to join the anterior cingulum at its centre. The internal cingulum is strongly marked and finely beaded. From it a series of fine ridges extends down the inner aspect of the lingual cusp. Both the anterior and posterior cingula are pronounced and are directly continuous with the internal cingulum. Besides its smaller size, this premolar differs from P $\underline{4}$ of *P. africanus* in its lower breadth index, the strong development of the internal cingulum, and the relative proportions of the two cusps.

M $\underline{1}$.—The trigon is clearly defined by ridges interconnecting the main cusps. It is relatively more expanded than in *P. africanus*, due mainly to a splaying outwards of the paracone and metacone. The trigon basin is relatively deep, and marked by secondary enamel wrinkles. The protocone is the largest cusp in the trigon, and the paracone is slightly larger than the metacone. The forward projection of the paracone leads to a slightly oblique disposition of the anterior margin of the crown, giving to the occlusal surface a somewhat rhomboidal shape. The hypocone is well developed and clearly demarcated by sulci from the protocone and metacone. The internal cingulum is strongly developed and beaded. It forms a projecting ledge which, as in *P. africanus*, appears to extend the occlusal surface of the crown inwards, since it is almost flush with the bottom of the trigon basin. It is continued without a break into the anterior cingulum in front, and posteriorly round the base of the hypocone. It does not project at the antero-internal angle of the crown to the extent seen in the holotype of *P. africanus*, nor is the anterior cingulum quite so broad. There is no protoconule. Finally, the base of the paracone is ridged by a distinct external cingulum.

Isolated Teeth of *Proconsul africanus*

Canine teeth.—Apart from the holotype and the skull of *P. africanus*, no maxillary or mandibular fragments have been found with the crowns of the canines intact. However, the roots are present in some cases, and in others the sockets, so that the general dimensions of the teeth in other specimens can be approximately inferred. A number of isolated canines have been collected on Rusinga Island and at Songhor which on the basis of size and the similarity of their morphology are here provisionally allocated to *P. africanus*. One of these, an upper canine from Rusinga (C.M.H.103, Rs.91) is illustrated in Pl. 3, fig. 15. It conforms closely with the upper canines of the skull of *P. africanus* (R.1948, 50). The total length of this specimen is 30 mm., and the maximum height of the crown is 11 mm. The antero-posterior diameter of the base of the crown is 8·6 mm., and the transverse 6·8 mm. The anterior aspect of the crown shows a flat faceted surface worn by contact with the upper lateral incisor, at the lower end of which is the remnant of a pronounced vertical groove. There is a well-marked internal cingulum.

Six isolated lower canines of approximately similar dimensions from Rusinga and Songhor are here also provisionally allocated to *P. africanus*. Their registration numbers are 645 (R.106a, 1947), C.M.H.18 (R.), C.M.H.19 (R.), 842, 1947 (Kathwanga), S.16, 1947, and S.D4. They are all characterized (like the lower canines in the skull R.1948, 50) by relatively low crowns. Some isolated upper canines of medium size may also possibly belong to the same species, but their identification presents considerable difficulty.

Incisors and canines.—In 1947 a series of ten associated teeth (R.342) were found on Rusinga Island at site R.1—the four upper incisors, the central lower incisors, and all four canines. All the teeth are badly weathered so that only approximate measurements can be taken from them. The estimated dimensions of the crowns of the incisors (average from the two sides) are as follows:

	Height	*Width*	*a.p.*
I $\underline{1}$	7·5 mm.	7·6 mm.	5·6 mm.
I $\underline{2}$	7·2 ,,	5·3 ,,	5·8 ,,
I $\overline{1}$	9·4 ,,	3·8 ,,	5·0 ,,

The lower canines are quite similar in form and dimensions to those of the skull of *P. africanus* and the central lower incisors also correspond closely in size. For these reasons, this collection of ten teeth may be assigned with some confidence to the same species.

The central upper incisors are spatulate. Posteriorly they show a well-marked cingulum and a centrally placed basal tubercle. The upper lateral incisors have asymmetrical crowns, with the free margin sloping up obliquely from a blunt apex towards the lateral aspect. They are small compared with the upper central incisors. The central lower incisors are slender, narrow teeth with a straight cutting edge. The lower canines are similar to those of specimen R.1948, 50. The details of the upper canines are obscured by much weathering; their total length averages 30 mm., the antero-posterior diameter of the crown is approximately 8·5 mm., and the transverse diameter 6·0 mm.

*C.M.H.*114 (*R.*), *S.*54, *and S.*13.—Three isolated central upper incisors which, on the basis of size and general proportions, are here referred provisionally to *P. africanus.*

*S.*410, 1948.—Right lateral upper incisor—almost a replica of the corresponding tooth in specimen 342.

Isolated Molars

1097 (*Kathwanga*).—An isolated last lower molar of the left side found at Kathwanga, excellently preserved and only slightly faceted by wear (Pl. 3, fig. 12). In general appearance it resembles M $\overline{3}$ in specimen C.M.H.102, but it is not so elongated and is slightly broader in front. The crown tapers behind into a narrow heel formed by the prominent hypoconulid. The width of the crown at the level of the tip of the metaconid is 8·7 mm., and at the level of the entoconid 7·8 mm. The protoconid and metaconid are of approximately equal size. The hypoconid is smaller and makes only a narrow contact at the centre of the talonid basin with the base of the protoconid. The entoconid is much reduced in size and marked on its central aspect by secondary enamel wrinkles. The hypoconulid is partly broken up into subsidiary cuspules. The external cingulum is well marked throughout its extent, and shows some fine beading.

*S.*405, 1948.—An isolated last molar of the left side, very similar to the last specimen (1097) except that it is smaller and relatively narrower. The external cingulum is also less distinct in its posterior half.

*C.M.H.*24.—The crown of a second right upper molar (unerupted) found at Songhor. The lateral cingulum is rather more strongly developed anteriorly than in the holotype of *P. africanus*, and the protoconule is very indistinct. In other details, however, the tooth is almost identical with the second molar of the holotype. The antero-posterior diameter of the tooth is 9·4 mm., and the transverse 10·4 mm.

S.2, 1947.—Left first upper molar (Pl. 3, fig. 13) only slightly worn. The main cusps are very sharply defined in this specimen. The hypocone, which approximates in size to the protocone, is continuous in front with the internal cingulum and the latter is not prolonged back on to the base of the cusp. There is a faint indication of a protoconule, and a trace of an external cingulum. The roots of the tooth are strongly divergent.

C.M.H.144 (*Rs*.).—A right first upper molar, very similar to the previous specimen, but slightly smaller and broader (Pl. 3, fig. 14). It appears to conform closely to the equivalent tooth in the holotype of *P. africanus*. The identification of this, and also of the other isolated upper molars here described, necessarily involves some element of doubt, since they show slight variations in details of enamel pattern which may possibly have some taxonomic significance.

C.M.H.143 (*Rs*.).—A slightly worn crown of a first left upper molar probably referable, on the basis of its dimensions and cusp pattern, to *P. africanus*. The hypocone is relatively large and broadly continuous with the internal cingulum, and the protoconule is only very faintly indicated. Its antero-posterior diameter is 8·2 mm., and its transverse 9·3 mm.

S.404, 1948.—A much worn upper molar provisionally assigned to *P. africanus* on the basis of its general proportions, but the identification is doubtful.

Deciduous Molars

C.M.H.141 (*R*.39).—A small fragment of the left alveolar process of a mandible with the first and second deciduous molars embedded in it. The teeth are severely weathered. The cusp patterns of the teeth are of the hominoid type, and are remarkably similar to those of the deciduous molars of a chimpanzee, but are much smaller. Their small size excludes them from *P. nyanzae* (as may be seen by comparison with the deciduous molars assigned to that species, Rs.258, and S.58), but appears to conform reasonably well with *P. africanus*. In any case, however, this identification must be regarded as provisional. The crown of the first deciduous molar is formed mainly by the large, conical buccal cusp, with a small indication of the lingual cusp on the medial side of its apex. There is a well-marked talonid, with a rudimentary hypoconid on its lateral margin, and the anterior margin of the crown is marked by a distinct anterior cingulum. The antero-posterior diameter of this tooth is estimated to be 6·4 mm., and the transverse diameter 4·4 mm. As already mentioned, the relative proportions and cusp pattern approximate very closely to those found in the chimpanzee. The second deciduous molar shows the five main cusps disposed in the usual hominoid pattern, a well-marked anterior fovea, and a suggestion of an external cingulum. Its estimated dimensions are about 8 mm. by 6 mm.

C.M.H.48.—(Locality unknown.) The crown of a first lower deciduous molar of the right side. It is almost a replica of the corresponding tooth in the previous specimen and is better preserved. The antero-posterior diameter is 6·4 mm., and the transverse 4·2 mm.

Table 3*

PROCONSUL AFRICANUS

Upper Dentition

	P $\underline{3}$			P $\underline{4}$			M $\underline{1}$			M $\underline{2}$			M $\underline{3}$			M $\underline{1}$/ M $\underline{2}$	M $\underline{2}$/ M $\underline{3}$
	a.p.	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*a.p.*
Holotype M.14081 (B.M.N.H.) .	7·3	9·4	129	5·8	8·9	152	7·9	9·6	122	9·2	11·3	123	7·8	10·2	130	86	118
R.1948, 50 . .	5·6	9·8	175	5·4	9·7	180	8·0	9·4	118	8·9	10·8	121	8·1	10·6	131	90	110
S.15, 1947 . .				5·6	7·0	125	8·2	7·6	93								
M.14085 (B.M.N.H.)							7·8	9·6	123								
C.M.H.24 . .										9·4	10·4	111					
C.M.H.143 . .							8·2	9·3	113								
S.2, 1947 . .							8·8	9·9	113								
C.M.H.144 . .							8·3	9·6	116								

Lower Dentition

	P $\overline{3}$			P $\overline{4}$			M $\overline{1}$			M $\overline{2}$			M $\overline{3}$			M $\overline{1}$/ M $\overline{2}$	M $\overline{2}$/ M $\overline{3}$
R.1948, 50 . .	9·0	5·8	64	6·0	6·4	107	8·1	7·2	89	10·0	8·8	88	11·0	9·1	83	81	91
C.M.H.102 . .				6·2	5·8	94	8·0	7·1	89	9·6	8·2	85	11·0	8·0	73	83	87
S.21 . . .				6·3	4·8	76	8·0	6·0	75	9·0	7·2	80				89	
1230, 1947 . .				6·8	6·2	91	7·7	6·6	86								
1097 . . .													10·8	8·7	81		
S.405 . . .													9·5	6·9	71		

[*] In the measurements listed in this and the following tables, where equivalent teeth are represented bilaterally the average of the two sides is given.

General Consideration of *Proconsul africanus*

Since *P. africanus* is now well known from its dentition and skull, and since it is the only Miocene ape of which a skull is at present available, it seems desirable to discuss the implications of certain of the characters of this species in further detail.

The size and light construction of the skull suggest that this extinct ape was a lightly built creature, and of relatively small size in comparison with the recent Ponginae. In their general dimensions the cheek teeth approximate to those of the chimpanzee, but the jaws are less massive. The incisor region of the upper jaw and the symphysial region of the mandible are also relatively narrower, so that the shape of the "muzzle" appears more pointed. With this character is associated a marked constriction of the lower extremity of the nasal aperture, giving rise to an appearance which resembles the catarrhine monkeys rather than the modern anthropoid apes. Other resemblances of the same type are also to be seen in the lateral view of the skull, for the proportions of the jaws relative to the calvaria, the marked prognathism, the light build of the zygomatic region, and the contour of the frontal region all combine to produce an impression which, apart from the size of the skull as a whole, is rather strongly suggestive of a skull of one of the smaller Cercopithecidae. The complete absence of a supra-orbital torus supported by a reinforcement of the lateral orbital margins, so characteristic of the skulls of the larger catarrhine monkeys and of the modern African apes, is a somewhat unexpected feature in a skull of the general dimensions of *P. africanus*, even if the specimen belongs to a female. This negative character is evidently related to the lightness of construction of the skull as a whole. Presumably, also, it is to be regarded as a primitive feature, and one which has been retained to some extent in the orang. In the latter, however, the contour and relative size of the orbits, as well as the morphological details of the supra-orbital region, are very different from those of *P. africanus*. In the fossil skull, the orbital region displays certain features which have a rather human appearance, but it is not to be inferred that *Proconsul* has any special relation to the Hominidae. Rather, it seems that these are basic features of the hominoid skull which have not been secondarily disturbed by such changes as the development of a strong supra-orbital torus. A similar consideration applies to the dimensions of the incisor teeth, for it is very doubtful whether the lower incisors, or the central upper incisors, of *P. africanus* are distinguishable from those of modern man; the hypertrophied and massively constructed incisors of the modern large apes are presumably, therefore, secondary developments which had not appeared in the early Miocene apes and which have been avoided in *Homo sapiens*. The relatively broad nasal bones of *P. africanus* are likewise to be regarded as primitive characters, and herein the resemblance is to the modern gibbons rather than to the large apes. On the other hand, there is no particular feature of the skull which can be taken to indicate special hylobatine affinities.

The possibility has been considered that the marked degree of prognathism shown in the skull of *P. africanus* may be partly the result of deformation during the process of fossilization. However, it is doubtful whether this is the case to any significant extent, for, apart from the fact that the maxillo-facial region on the right side appears to have escaped distortion, the proportions of the body and ascending ramus of the mandible are by themselves consistent with a pronounced prognathism.

Although the back part of the skull is missing, the total volume of the brain-case must have been small in proportion to the size of the jaws. A primitive degree of cerebral development is further indicated by certain features of the endocranial aspect of the skull. In particular, the presence of a deep and well-defined subarcuate fossa and a broad vermiform fossa indicate that the proportions of the cerebellum evidently resembled those of catarrhine monkeys rather than the modern large apes. In the latter, the enlargement of the cerebellar hemispheres has produced a secondary withdrawal of the petrosal lobule from the subarcuate fossa and a submergence of the inferior vermis. In the course of the evolutionary development of the brain, the progressive enlargement of the cerebellar hemispheres has proceeded *pari passu* with the expansion of the cerebral cortex (under the influence of the important cortico-ponto-cerebellar connections), and it may thus be supposed that in *P. africanus* the cerebral hemispheres had not undergone the expansion characteristic of the recent

Ponginae. There is confirmatory evidence for this inference, for the convolutional impressions on the frontal bone indicate clearly that the fissuration of the frontal lobe was quite simple. Further, if our identification of the position and extent of the central sulcus is correct, the frontal lobe as a whole must have been relatively small. In these features, again, and also in the apparent disposition of the anterior end of the intra-parietal sulcus, the brain of *P. africanus* shows remarkable resemblances to that of the cercopithecoid monkeys.

In general, then, although the dentition of this Miocene ape conforms entirely in all its fundamental features to that characteristic of the Hominoidea, the skull preserves a number of primitive features which, by themselves, might be taken to indicate cercopithecoid affinities. The implication of this combination in *P. africanus* of primitive and advanced characters will be discussed later.

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(see p. 12 for diagnosis)

In the course of studying the hominoid fossils recently collected in Kenya, it soon became apparent that some of the jaws and teeth which had been provisionally referred to *P. africanus* differ from the holotype not only in their larger size, but also in certain morphological details, and that these differences are sufficiently marked to require taxonomic distinction. However, since the teeth resemble *P. africanus* in the general feature of their cusp pattern, the differences are believed to be of not more than specific value. We take as holotype of the species, *P. nyanzae,* the maxilla and upper dentition found at Rusinga in 1932 (C.M.H.2, R.I.A.), described and figured by MacInnes in 1943 (pl. 24, fig. 1; pl. 25, figs. 1, 2).

A number of jaws (or fragments of jaws) and teeth referable to this species have now been collected, including the 1942 mandible discovered on Rusinga Island. The mandible found at Koru and described by Hopwood (1933*a*) as *P. africanus* should also be assigned to *P. nyanzae.* Before describing the individual specimens of *P. nyanzae,* it is convenient to give a general account of the dentition, based on the holotype and certain other available material. Included in the latter are specimens of associated upper and lower teeth (C.M.H.2–R.1, and C.M.H.4–R.1) previously described by MacInnes (and illustrated in pl. 24, figs. 6 and 7 of his paper, 1943).

Upper dentition (Pl. 4, figs. 16–18).—The central incisors are preserved in specimen C.M.H.3 and have been described in detail by MacInnes. In dimensions and shape they have a remarkably human appearance and are similar to those of *P. africanus* except for their slightly larger size. In contrast with the chimpanzee material which is available to us for comparison, they are conspicuously smaller in absolute dimensions and also smaller relatively to the rest of the dentition. They have a spatulate form with a straight cutting edge approximately 8 mm. wide. The concave lingual surface is bounded at each margin by a ridge of enamel which, at the base of the crown, converges to join the cingulum. Immediately adjacent to the cingulum is a small basal tubercle from which a broad low ridge extends down towards the cutting edge. The whole of the concave lingual surface is furrowed by fine longitudinal enamel ridges. Five isolated central incisors found at Rusinga, C.M.H.112 (R.31), C.M.H.115 (R.110), C.M.H.9, C.M.H.10, and C.M.H.113 (R.), one at Songhor (S.54, 1948), and one found on Maboko Island (C.M.H.11) are so similar in their dimensions and morphology to those of specimen C.M.H.3 that they may be provisionally assigned also to *P. nyanzae*. Two of these teeth (C.M.H.9 and C.M.H.10) are shown in Pl. 4, fig. 23. These illustrations serve to demonstrate the main morphological features of the teeth without further description. The following are the principal dimensions of the crowns in all these specimens. The antero-posterior measurement (a.p.) is taken between the central point of the cingulum at the base of the crown behind, and the centre of the upper margin of the anterior surface of the crown.

	Height	*Width*	*a.p.*
C.M.H.112 . . .	10·0 mm.	8·3 mm.	6·3 mm.
C.M.H.9 . . .	10·8 ,,	9·8 ,,	7·0 ,,
C.M.H.10 . . .	10·8 ,,	8·4 ,,	6·8 ,,
C.M.H.11 . . .	11·0 ,,	9·6 ,,	7·2 ,,
C.M.H.3* . . .	9 ,,	8 ,,	6 ,,
C.M.H.115* . . .	11 ,,	9 ,,	7 ,,

* In these specimens, which have been exposed to weathering, measurements are given to the nearest millimetre.

The right and left lateral incisors of *P. nyanzae* were found with the maxillary fragment No. 712, 1947 (*vide infra*). The crown is considerably smaller and narrower than that of the central incisors and is conical rather than spatulate. The anterior surface is markedly convex from side to side; the lateral margin extends obliquely downwards and medially to terminate in a blunt point on the cutting edge of the tooth; the basal cingulum is pronounced. Further morphological details can be seen by reference to text-fig. 7. The dimensions of the crown of the better preserved left lateral incisor are: Height 8 mm.; Width 5 mm.; Antero-posterior 6 mm.

The upper canines form large and powerful tusks, characterized by a sharply defined posterior margin and a deep longitudinal groove on the anterior aspect. The cingulum is fairly well marked on the lingual surface of the base, and behind forms a small "heel" (basal tubercle) where it is met by the upper end of the posterior margin of the tooth. The height of the crown of the upper canine in known specimens varies from 20–24 mm.

The upper premolars are relatively stout bicuspid teeth, the cusps being blunter and more rounded than in *P. africanus*. Because of wear or weathering, the details of the enamel pattern are not easily discerned in the holotype and specimen C.M.H.3. The contrast in the size and height of the labial and lingual cusps is by no means so pronounced as in *P. africanus*, and in $P\underline{4}$ they are sub-equal. The anterior and posterior cingula are distinct, and the two cusps are joined by a transverse ridge which is situated approximately in the centre of the occlusal surface.

In all the upper molars the internal cingula are strongly developed. In contrast to *P. africanus*, the anterior cingulum is relatively narrow and less distinct, the internal cingulum at the antero-internal angle of the crown is not extended into such a prominent ledge, but the posterior cingulum is more distinct and tends to be conspicuously beaded. The internal cingulum is relatively narrower and is situated more on the side of the crown than in *P. africanus*, and thus does not give the same appearance of extending its occlusal surface. The main cusps of the trigon are also larger relatively to the occlusal surface as a whole, more massive with a broader base, and less acutely pointed. The protocone is the most bulky of the three cusps of the trigon. Compared with it, the hypocone is usually smaller. The crests connecting the cusps are not so clear cut, particularly that joining the protocone and paracone. The latter shows the slight forward angulation seen in *P. africanus*, with the formation of a definite, small, rounded protoconule at its junction with the anterior cingulum. In *P. africanus*, as already noted, this cuspule is represented by hardly more than a slight thickening at the angulation of the crest. In the first and second molars the hypocone tends to be separated from the internal cingulum by a well-marked furrow. In the third molar it is broadly continuous with the internal cingulum, as it is in all the molars—and particularly in M $\underline{1}$—of *P. africanus*. The third molar shows some reduction in size, but though the hypocone is relatively smaller than in the first and second molars, the other three cusps are quite well defined. In the second and third molars, the cingula (particularly the internal cingulum) may be quite elaborately beaded, the "beads" being associated with fine crinklings of the enamel which extend in parallel arrangement down the slopes of the protocone and hypocone. These delicate crenations may extend into the floor of the trigon and also along the posterior aspect of the crista obliqua (see Pl. 5, figs. 24–28). They lead to an intricate pattern which surpasses in its complexity the secondary foldings seen in *P. africanus*. An external cingulum is also present in all the upper molars, but it is rudimentary in appearance and evidently variable in its extent. The dimensions of the upper premolars and molars in available specimens of *P. nyanzae* are given in Table 4.

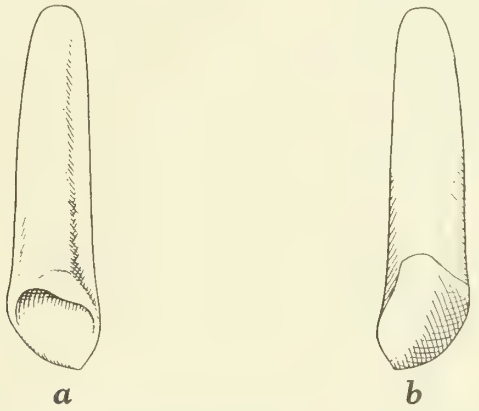

FIG. 7. Upper left lateral incisor of *P. nyanzae* (712, 1947), viewed from (a) lingual aspect, (b) labial aspect. × 2.

Five isolated upper molars are referable to *P. nyanzae*. Of these the most striking is the crown of an unerupted left upper molar (C.M.H.33), the locality of which is not precisely known. From its rounded contour and the relative size of the hypocone, it is evidently a third molar (Pl. 5, fig. 27). The lateral surface of the tooth, including the paracone and metacone, has undergone some abrasion in the course of fossilization. The crenation of the internal cingulum is particularly elaborate in this tooth. The protocone-paracone crest is merged with the anterior cingulum at its forward angulation, and the hypocone is separated from the postero-internal cingulum by a well-marked furrow. The crown of a second left upper molar, C.M.H.32 (R.39), is not quite so elaborately folded (Pl. 5, fig. 28). It has, however, undergone some weathering which may have obscured some of the finer details of the enamel pattern. The protocone is the largest of the three cusps of the trigon. There is a small protoconule, and the posterior cingulum is beaded and particularly distinct. This tooth is somewhat smaller than the second molars of the holotype, but considerably larger and more robust than the corresponding tooth of *P. africanus*.

The crowns of two unerupted upper molars found exposed in surface deposits on Rusinga Island (Pl. 5, figs. 25, 26) are identified as a first right molar C.M.H.121 (Rs.39) and a second right molar C.M.H.122 (Rs.). In both specimens the four main cusps are relatively large and have rounded apices. The trigon is not so clearly demarcated as in *P. africanus*, and the crests joining the protocone to the paracone and metacone are much less distinct, being interrupted by secondary foldings. The internal cingulum is strongly developed and the beading gives it a closely serrated appearance. The posterior cingulum is clearly differentiated, and in the second molar is beaded. A second left upper molar from Songhor (C.M.H.34), moderately worn, resembles very closely that of the holotype.

Lower dentition (Pls. 4, 5, figs. 19, 22, 29–33).—No lower incisors certainly referable to *P. nyanzae* are present in the series available for study. The dimensions of the root sockets in the 1942 mandible are given by MacInnes as follows:

	a.p.	*Width*
Right I $\overline{1}$	6·8 mm.	4·0 mm.
I $\overline{2}$	8·0 ,,	4·5 ,,
Left I $\overline{1}$	6·6 ,,	4·0 ,,
I $\overline{2}$	7·4 ,,	4·5 ,,

All the specimens of the symphysial region of the mandible so far available demonstrate that the lower incisors were implanted in a fairly vertical position.

The lower canine is a relatively large tooth, implanted almost vertically in the mandible (as viewed from the lateral aspect) and not diverging laterally to the extent characteristic of the modern large apes (see text-figs. 9, 29). The internal cingulum is quite distinct, and continues postero-medially into a small basal tubercle. At the alveolar margin the canine is separated from the lateral incisor by a small diastema of 2 or 3 mm. The height of the crown of the lower canine in known specimens varies from 15 to 19 mm.

The anterior premolar, P $\overline{3}$, is of the sectorial type, and varies considerably in size in different specimens. In the 1942 mandible its length is about 9·0 mm., but greater in other specimens. It is presumed that these are sexual differences, but the weathered condition of the teeth in the 1942 mandible renders accurate measurement impossible. P $\overline{3}$ is set obliquely, its long axis making an angle, which varies approximately from 45° to 60°, with the axis of the premolar-molar series. It has a small talonid, the basin of which is continued up on to the postero-internal aspect of the main cusp as an elongated groove. In the larger teeth of the Koru mandible (M.14086), traces of small labial and lingual cuspules are present on the talonid. The posterior premolar, P $\overline{4}$, is bicuspid, the cusps either being equal in size, or the lateral slightly the larger. There is a well-marked anterior fovea, and a rather deeply cupped talonid with very small labial and lingual cuspules.

The first lower molar is characterized by its small size in comparison with the second molar. The relatively small size of the first lower molar is a common feature of the Dryopithecinae generally, but the contrast is more marked in *Proconsul* than in the dryopithecine types of Europe and India (see Table 6). The tooth is rectangular in shape with a length-breadth index which varies from 85 to 92. The talonid in seven specimens is slightly wider than the trigonid. In one other specimen it has the same width. A well-developed hypoconulid is present in addition to the four main cusps, and is either situated in the central axis or slightly to the buccal side. The metaconid is the largest cusp and the entoconid is considerably smaller than the hypoconid. The protoconid is very slightly in advance of the metaconid. All the cusps are clear-cut pyramidal eminences with little or no secondary furrowing. A small external cingulum is present which is rather variable, but better marked in relation to the trigonid. It may run into continuity with the anterior cingulum which borders the anterior fovea. The sulci separating the cusps conform to the "*Dryopithecus*-pattern" of Gregory (1916). The anterior fovea is a well-defined fossa, and there is a small posterior fovea between the entoconid and hypoconulid.

The second lower molar is a large tooth, with an antero-posterior measurement ranging from 10·3 mm. to 13 mm. The metaconid is the largest of the cusps, but may be equalled by the hypoconid. The entoconid is relatively small and may even be smaller than the hypoconulid. The hypoconulid is slightly to the buccal side of the median axis of the crown. The anterior part of the external cingulum is well marked, and posteriorly is represented by a notch at the lower end of the sulcus between the hypoconid and hypoconulid. In one isolated specimen, C.M.H.31 (R.31), an unerupted tooth, the external cingulum shows a distinct beading (Pl. 5, fig. 33). The anterior fovea is relatively large and there is also a very distinct posterior fovea. In the unerupted tooth there is some secondary wrinkling on the central aspect of the cusps, particularly on the metaconid. In five out of seven specimens, the talonid is slightly wider than the trigonid.

The third lower molar is an elongated and somewhat triangular tooth, narrowing posteriorly into a blunt point formed by the backward extension of the hypoconulid. The metaconid is the largest cusp, the entoconid is relatively small, and the hypoconid and hypoconulid are of approximately equal size. Secondary wrinkles are present in the talonid basin, and also along the ridge connecting the metaconid with the entoconid at the inner margin of the occlusal surface. The external cingulum is well marked anteriorly; in one specimen from Kathwanga (143, 1947) it is continuous along the whole lateral surface of the crown and is distinctly beaded. The anterior fovea is not so well developed as in the first and second molars, but there is a large circumscribed posterior fovea between the entoconid and hypoconulid. The hypoconulid is to the buccal side of the median axis of the crown and in approximate alignment with the protoconid and hypoconid.

The dimensions of the lower premolars and molars in available specimens of *P. nyanzae* are given in Table 5.

Consideration of Individual Specimens of P. nyanzae.—The description of the dentition of *P. nyanzae* given above is based primarily on the holotype and specimens

C.M.H.3 and C.M.H.4, with reference also to other material identified as belonging to the same species. Certain details of the teeth and jaws of some of the individual specimens will now be considered separately.

C.M.H.2 (R.1A).—This specimen, the holotype of the species *P. nyanzae*, consists of the maxillary region of the face, considerably crushed, with most of the upper dentition. The teeth are excellently preserved but much worn (Pl. 4, figs. 16, 20). The specimen has already been described in detail by MacInnes (1943). Some of the outstanding features to which he drew attention may be briefly recapitulated. In general size, the facial skeleton must have approximated closely to that of a fairly large male chimpanzee. The nasal aperture is relatively much narrower than in the recent large apes and the sub-nasal prognathism must have been considerably less. The diastema between the lateral incisor and the canine is not more than 5 mm. The palate is relatively broad, the width between the inner margins of the canines being 31 mm., and between the inner margins of the first molar crowns 34 mm.

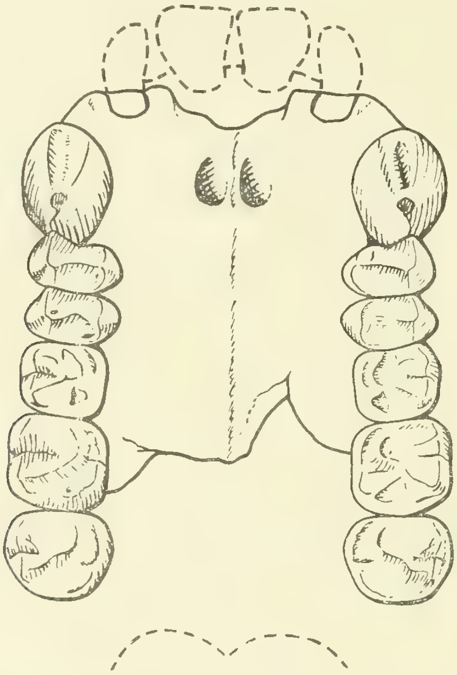

FIG. 8. Graphic reconstruction of the palate and upper dentition of *P. nyanzae* (C.M.H.2). Natural size.

A reconstruction of the palate has been drawn (text-fig. 8) by making corrections for the distortion produced by fracture of the specimen and placing the premolar-molar series in their proper alignment, and by reproducing symmetrically features which are preserved on one or the other side. It is not possible to ascertain the precise position of the posterior margin of the palate, but the anterior limit is approximately indicated by the presence of the sockets for the lateral incisors. The tooth rows probably did not show more than a slight degree of divergence posteriorly. The contours of the incisor teeth are based on isolated specimens. The palate is relatively large, and the canines are powerful teeth separated from the lateral incisor on each side by a well-marked diastema. A comparison of text-fig. 8 with the photograph (Pl. 2, fig. 4) of the palate of *P. africanus* in the skull (R.1948, 50)—even allowing for the distortion of the latter—makes it clear that there is a strong contrast in absolute size between these two species.

Rusinga mandible 1942 (*R*.1).—This almost complete mandible, discovered on Rusinga Island in 1942, has been described and figured by Leakey (1943) and MacInnes (1943). The teeth of the premolar-molar series are not so large as in the other specimens of *P. nyanzae*. They are also relatively small in comparison with the size of the mandible (text-fig. 9), and particularly in relation to the height of the horizontal ramus (text-fig. 10). The details of the cusp pattern have unfortunately been obscured by wear and weathering, but in general they appear to conform with those of specimen C.M.H.4. The canine, however, though smaller in absolute size, is conspicuously larger in comparison with the premolar and molar teeth. The anterior premolar, also, is markedly reduced and the contrast in size between the first and second molars is less obtrusive. The crown of the third molar is more rectangular in shape (particularly on the right side), the width of the talonid differing but little from that of the trigonid, and the hypoconulid in this tooth is more median in position.

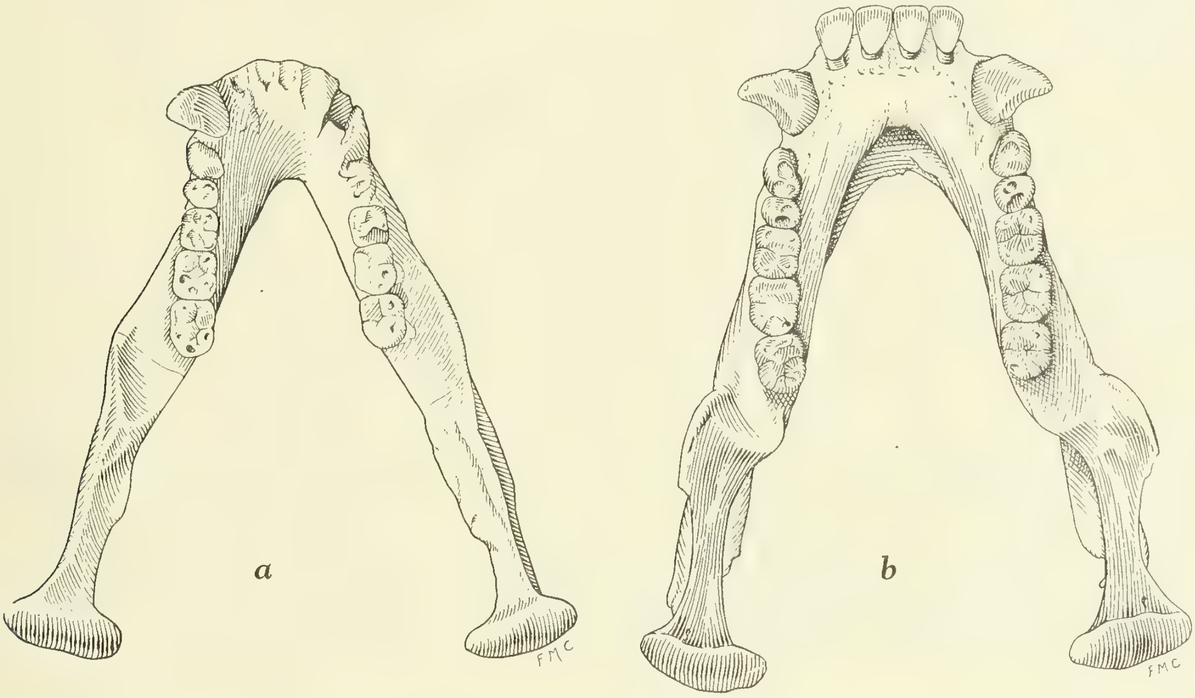

Fig. 9. A. 1942 mandible of *P. nyanzae* viewed from the occlusal aspect of the teeth, compared with B. the mandible of a male chimpanzee. × ⅔.

The sockets for the incisors indicate that the latter were implanted in an almost vertical position and that, compared with the modern large apes, they were relatively small. A diastema of 3 mm. width separates the canine from the lateral margin of the socket for the lateral incisor. The over-all width of the incisor sockets is not more that 19 mm., compared with a similar measurement of 29 mm. in a male chimpanzee with a jaw of equivalent general dimensions. This narrowness of the incisor region is characteristic of all those Dryopithecinae in which the symphysial region of the mandible is known. It appears, therefore, that the enlarged incisor series, leading to a broadening out of the symphysial region, which is a characteristic feature of the modern large apes, is to be regarded as a secondary acquisition. In the large apes of Miocene and Pliocene times, the narrowness of the incisor region is related to certain other features of the mandible. These are, a slight convergence of the premolar-molar series in a forward direction, the absence of a simian shelf, and a slope of the median axis of the symphysis which approaches the vertical. In these features, indeed, the mandible of these fossil apes contrasts less with the human jaw than does that of recent Ponginae, and at the same time resembles the jaws of some Cercopithecoidea. It seems probable that the simian shelf in the modern large apes is simply the result of the secondary widening of the symphysial region for the accommodation of hypertrophied incisors, and perhaps serves a mechanical function in strengthening this part of the mandible.

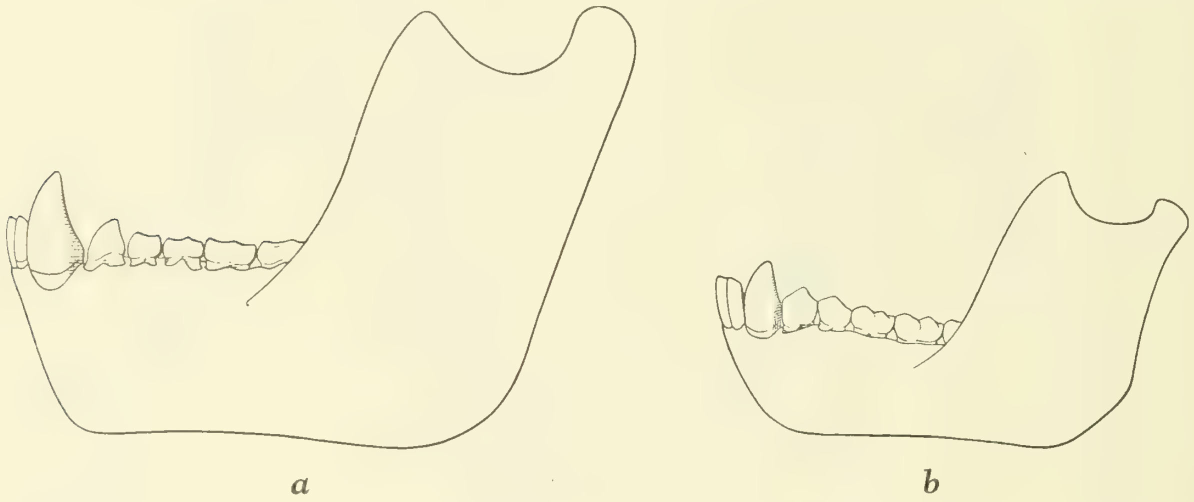

Fig. 10. A. Lateral view of the 1942 mandible of *P. nyanzae*. Corrections have been made for the weathering of the teeth by reference to other specimens of *P. nyanzae*, and the outlines of the incisor teeth have been added. The vertical ramus has also been slightly reconstructed. B. Lateral view of the mandible of *P. africanus* (R.1948, 50). × $\frac{2}{3}$.

A further interesting feature of the Rusinga 1942 mandible is the bicondylar width of 112 mm. In the male chimpanzee mandible also shown in text-fig. 9, the bicondylar width is 110 mm. Thus, though the total width of the alveolar region of the mandible and the size of the teeth are much smaller in the fossil specimen, the width of the base of the skull was evidently equivalent to that of the male chimpanzee. This is related to a marked posterior divergence of the ascending rami of the *Proconsul* mandible. Attention has already been drawn to the relatively great height of the ascending ramus (Leakey, 1943). This, combined with the relative shortness of the alveolar border indicates that the whole facial region must have been more abbreviated than it is in the recent large apes as, indeed, is also shown by the facial fragment C.M.H.2.

Text-fig. 10A is a drawing of the lateral view of the 1942 mandible of *P. nyanzae*, slightly reconstructed to make correction (by reference to other specimens of the lower dentition of the same species) for the weathering of the teeth, and also to show the probable appearance of the incisors. The exact details of the contour of the ascending ramus are somewhat conjectural owing to its rather poor state of preservation, but its main dimensions seem to be well assured by the contacts of the portions which are preserved. The drawing makes clear the relative shortness of the body of the mandible in comparison with the height of the ascending ramus. The drawing of the mandible of *P. africanus* (text-fig. 10B) emphasizes the contrast between this and the mandible of *P. nyanzae*. Apart from its smaller general size, the former is strongly distinguished by the more sloping symphysial contour, the shape of the body and the relatively lower ascending ramus. The contrast is the more impressive since the total length of the premolar-molar series in the 1942 mandible, as already noted, is less than that of the other specimens of *P. nyanzae* and indeed is not much greater than in *P. africanus*. From the mandibular contours *P. nyanzae* must have been considerably less prognathous than *P. africanus*.

For the main measurements of the Rusinga 1942 mandible, reference should be made to MacInnes' monograph (1943). The relatively small dimensions of the dentition in this mandible originally suggested that it might harmonize more closely with the holotype of *P. africanus* than that of *P. nyanzae*. However, apart from the discovery of the skull of *P. africanus* in 1948, which has now made it clear that the mandible in that species is very different in build and proportions (text-fig. 10), a portion of the maxilla (712, 1947) belonging to the same individual as the 1942 mandible, and containing all the premolar and molar teeth, was found at the same site in 1947. The teeth in this maxillary fragment (Pl. 4, fig. 18), though somewhat smaller, conform closely in their proportions and shape with those of the holotype of *P. nyanzae*. The details of this specimen are as follows. The occlusal relationships are sufficiently accurate to make it certain that they belong to the same individual, particularly since erratic and asymmetrical wear of the first molar reflects a type of abnormality which MacInnes has noted to be also present in the right first molar of the mandible. All the teeth are considerably worn, the occlusal surfaces of the second and third molars being flat. No details of the cusp pattern can, therefore, be made out. The remains of the internal cingulum are just visible, and there is also a well-developed external cingulum. The first molar is relatively small compared with the second, and the last molar shows no significant reduction (herein contrasting rather strongly with *P. africanus*). The premolar and molar teeth in this specimen are a little smaller than in specimen C.M.H.4 (though they are distinctly larger than the known specimens of *P. africanus*). This is probably a sexual difference, since the relatively small dimensions of the lower dentition are associated with a large mandible of a size equivalent to that of other specimens of *P. nyanzae*. The base of the zygomatic process is not included in the maxillary fragment, but it clearly had its origin much further away from the alveolar border than in *P. africanus*, indicating an upper jaw of larger size. The lateral incisors found in association with the maxillary fragment have been described above. There is also a much worn left central incisor, the crown of which has been ground down almost to the level of the cingulum. The maximum width of the remaining portion of the crown is 8 mm.

S.28, 1947 (Pl. 4, fig. 21; text-fig. 11).—The body of the left half of a mature mandible found at Songhor. The roots of the teeth are all in position, as well as the basal half of the crown of the canine. Apart from the latter, the crowns of all the teeth are missing. The outer surface of the bone has been exposed to weathering and has partly flaked away. The symphysis is massive, being 40·2 mm. in vertical diameter and 23·6 mm. at its maximum thickness in antero-posterior diameter. There is no simian shelf. The thickness of the symphysis is evidently related to the need for accommodating the roots of the large canines which, because of the narrowness of the incisor region, approach the median plane rather closely. The median axis of the symphysis makes an angle of approximately 70° with a horizontal line passing through the lowest point of the symphysis and the lower border of the body of the mandible. Compared with *Dryopithecus* (Smith Woodward, 1914, Gregory & Hellman, 1926) the symphysial region of the mandible is distinguished by its much greater thickness (the centre of its posterior aspect being produced back well beyond its lower border), and in the more vertical direction of the median axis of the symphysis.

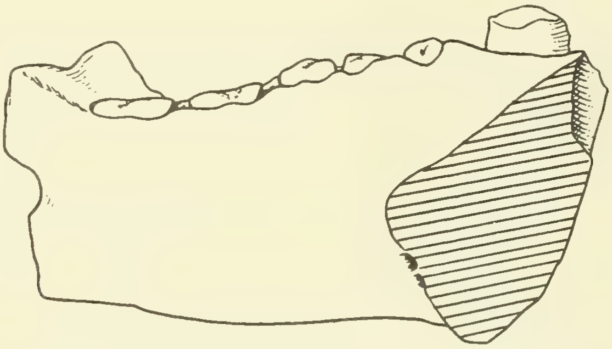

FIG. 11. The body of the left side of the mandible of *P. nyanzae* (S.28, 1947) viewed from the medial aspect. The teeth have been broken off close to the alveolar border. In front, the socket for the left central incisor has been exposed. Note the massive symphysis, the broken surface of which is exposed almost exactly in the median plane. Natural size.

The body of the mandible is also striking for its massiveness, particularly when compared with the mandible of a chimpanzee with a tooth-row of equivalent length. The height of the body at the level of the first molar tooth is 31·0 mm.; its maximum thickness opposite the last molar is 20·5 mm. The anterior border of the vertical ramus overlaps the position of the posterior half of the last molar crown, and extends downwards and forwards as a rounded ridge as far as the level of the first molar tooth. The single mental foramen is large, and is situated at the level of the interval between the two premolar teeth. The lower border of the mandible is thick and rounded. On the medial aspect of the body of the mandible an ill-defined mylohyoid ridge can be traced forwards to the convexity of the posterior aspect of the symphysis.

The roots of the incisor teeth are laterally compressed and implanted almost vertically. The proportions of the canine and post-canine teeth, so far as they can be assessed from the dimensions of the roots, correspond closely with those of specimen C.M.H.4. A reconstruction of the mid-line of the whole mandible makes it clear that the lines of the premolar-molar series of the two sides must have converged slightly in an anterior direction, as they do in the 1942 mandible.

*C.M.H.*111 (*R.*).—A weathered fragment of the left side of a mandible, including the symphysial region and the anterior part of the body. The crowns of P $\overline{4}$ and M $\overline{1}$ are preserved, and part of that of P $\overline{3}$. The root of the canine is in position, but the sockets for the incisor teeth are obscured by encrustation. The symphysis is rather less massive than in the previous specimen, but its median axis shows approximately the same degree of inclination, and there is no simian shelf.

*C.M.H.*5 (*R.*1).—The body of the left half of a mandible of an immature individual (text-fig. 12), described by MacInnes (1943, p. 170). P $\overline{4}$, M $\overline{1}$, and M $\overline{2}$ are in position and, though affected by weathering, appear to be almost unworn by use. The socket for the last molar indicates that this tooth had almost certainly not completed its eruption and (as MacInnes has pointed out) this inference is confirmed by the absence of a pressure facet on the posterior surface of M $\overline{2}$. On the other hand, the position of the massive root of the canine, still embedded in its socket, makes it clear that this tooth, even if still in course of eruption, must have almost completed this process. The lower end of the anterior border of the ascending ramus entirely overlaps the socket for M $\overline{3}$ on the outer side. The height of the body of the mandible at the level of M $\overline{2}$ is 24 mm.

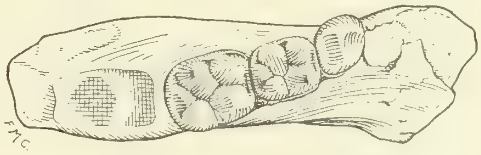

FIG. 12. Left side of the body of the mandible of *P. nyanzae* (C.M.H.5) viewed from the occlusal aspect of the teeth. P $\overline{4}$, M $\overline{1}$, and M $\overline{2}$ are in position. Behind M $\overline{2}$ is seen the socket for the incompletely erupted M $\overline{3}$. Natural size.

*C.M.H.*7 (*R.*30).—Fragment of body of left half of mandible, with P $\overline{4}$ and M $\overline{1}$ (considerably worn) in position, and the roots of P $\overline{3}$.

600 (*R.*106).—Fragment of body of right half of mandible, with P $\overline{4}$ and M $\overline{1}$ in position, and the roots of P $\overline{3}$. The specimen has been exposed to a moderate degree of weathering.

*C.M.H.*110 (*R.*5).—An important although poorly preserved mandible of an immature individual with P $\overline{4}$ and M $\overline{2}$ present on both sides, the posterior half of the crown of M $\overline{1}$ on the left side, the roots of dm $\overline{1}$, and the roots of the permanent incisors and temporary canine of the left side (Pl. 4, fig. 22). A brief description of it was given by MacInnes in 1943.

The first permanent molar is fully erupted and shows small but quite well-marked attrition facets on the central aspects of the hypoconid and entoconid. The second permanent molar on each side is incompletely erupted and quite unworn (Pl. 5, fig. 32). On the left side the anterior part of the crown is about 1 mm. below the level of the crown of M $\overline{1}$. On the right side the posterior margin of the crown is still embedded in the base of the vertical ramus of the mandible (as was probably also the case on the left side in the complete, undamaged, mandible). The posterior premolar is in process of eruption, apparently at about the same stage as M $\overline{2}$. The root of the left temporary canine is relatively small, measuring 7·4 mm. in antero-posterior diameter and 4·2 mm. in transverse. From the disposition of the roots, it is evident that the incisors and canines are set rather more obliquely than in the adult mandible, but this may be partly the result of distortion. The tip of the right permanent canine has been exposed by a break in the specimen. It is deeply embedded in the jaw, at least 7·0 mm. below the level of the alveolar margin. A radiographic examination of the specimen clearly shows the crown of the anterior premolar embedded in the jaw, and thus a few millimetres below the level of the posterior premolar. It is a large tooth of sectorial type similar to (but not quite so large as) the corresponding tooth in specimen C.M.H.4.

From this specimen it is evident that in *Proconsul nyanzae* the posterior premolar and the second molar erupted at about the same period, a little earlier than the anterior premolar, and some considerable time before the eruption of the permanent canine. The order of eruption thus appears to have been comparable to that of the modern chimpanzee (in which, also, the posterior premolar may erupt in advance of the anterior—Schultz, 1935). A comparison of the specimen with the mandible of a chimpanzee of equivalent dental age (text-fig. 13) emphasizes the contrast shown in the incisor region. In the fossil mandible the symphysial region is much narrower (in association with the smaller size of the incisor teeth) and the front of the mandible is correspondingly attenuated.

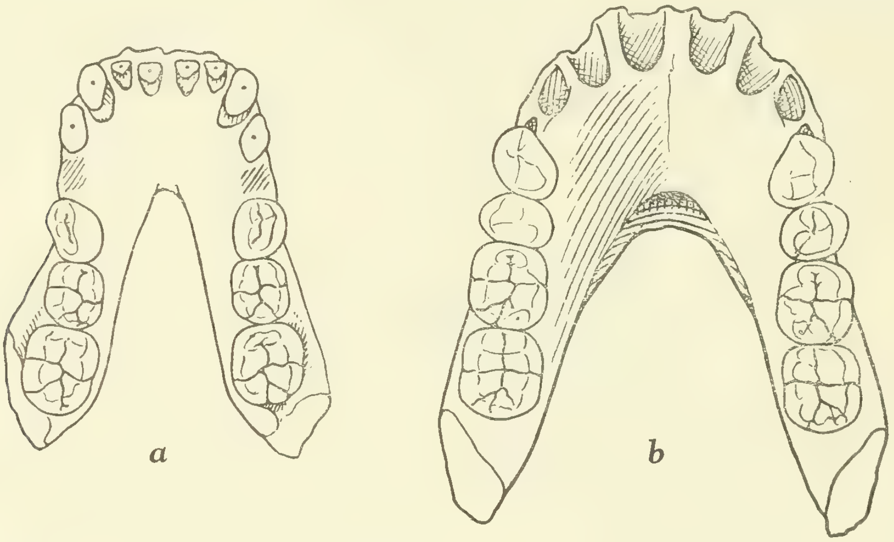

Fig. 13. A. Graphic reconstruction of the mandible of an immature specimen of *P. nyanzae* (C.M.H.110) compared with
B. The mandible of an immature chimpanzee of equivalent dental age. Note the relatively small size of the first molar in the *Proconsul* mandible. Natural size.

993, 1947.—Part of an immature maxilla found on Rusinga Island in the region of Survey Beacon No. 2, near Kiahera Hill. It has been exposed to weathering, but is otherwise almost complete on the left side except for the zygomatic process and frontal process (text-figs. 14, 15). The whole of the left half of the palate is also preserved. The two deciduous molar teeth and the first permanent molar are in position. The biting edge of the unerupted first permanent incisor tooth is just visible deep in the margin of the alveolus. The temporary canine is represented only by its socket; in an X-ray photograph of the specimen, the crown of the permanent canine can be seen embedded in the maxilla with its tip about 7 mm. above the alveolar margin. A portion of the crown of the second permanent molar, buried deeply in the region of the maxillary tuberosity, is partly exposed where the bony wall of the maxilla has broken away. The occlusal aspect of the unerupted tooth faces almost directly backwards.

The deciduous molars and the erupted first permanent molar have unfortunately been much affected by weathering and the details of the cusp pattern thus obscured. The first deciduous molar is bicuspid, the labial being considerably larger than the lingual cusp. The second deciduous molar has a well-defined trigon, separated from the hypocone by a clear-cut ridge connecting the protocone with the metacone. The hypocone is a little smaller than the other three cusps. Because of the effects of weathering, it is not possible to ascertain with any accuracy the dimensions of these teeth. The width of the biting edge of the first permanent incisor is estimated to be at least 8·5 mm.

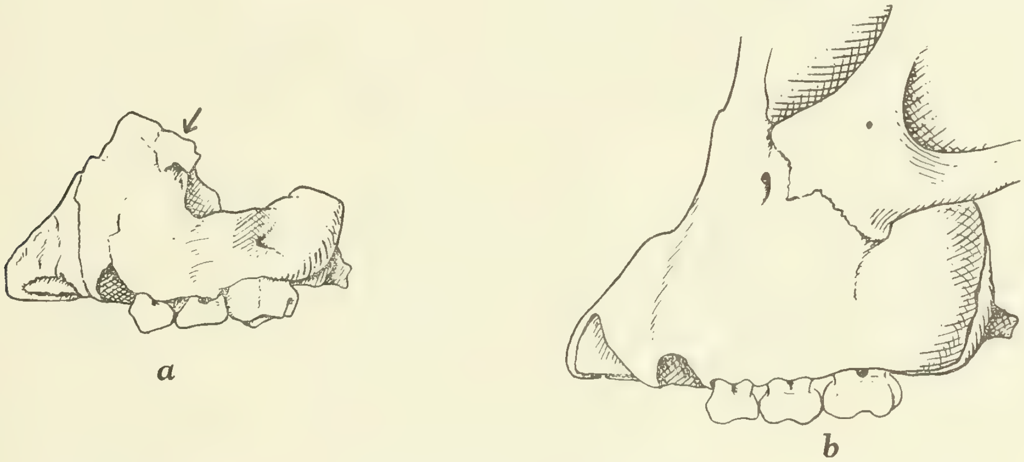

Fig. 14. A. The left maxilla of an immature specimen of *P. nyanzae* (993, 1947), compared with B. The left maxilla of a young chimpanzee of equivalent dental age. In the fossil specimen, the two deciduous molars and the first permanent molar are in position, and in front the cutting edge of the first permanent incisor is just appearing. An arrow points to a small portion of the inferior margin of the orbit, below which is seen the infra-orbital foramen. Natural size.

After completing the superficial examination of the specimen and preparing text-figs. 14 and 15, the crown of the unerupted second molar was fully exposed and freed from its alveolar cavity. The crown is well preserved and clearly shows all the secondary details of the enamel pattern (Pl. 5, fig. 24). In dimensions and proportions, it is very near to the second upper molar of *P. nyanzae* (see Table 4), and closely resembles the isolated molar found at Rusinga (C.M.H.32) depicted on Pl. 5, fig. 28. The protocone is conspicuously larger than the other cusps of the trigon, and the hypocone is relatively small. At the junction of the rounded anterior border of the protocone with the anterior cingulum is a small, but distinct, rounded protoconule. The anterior cingulum forms a narrow rim which is continued round the base of the protocone directly into the beaded internal cingulum. The latter, again, extends on to the base of the hypocone and links up with a well-defined posterior cingulum.

The premaxillary element is demarcated by a suture which is visible on the palate and also on the facial aspect of the bone. Compared with a young chimpanzee of equivalent dental age, this element is relatively smaller. The margin of the lower part of the nasal aperture is not very clearly defined, but the aperture was evidently rather narrow. Its maximum breadth can be obtained by reference to the mid-line of the palate which is preserved over its posterior three-quarters, and is estimated to be not more than 11 mm. The infra-orbital foramen is small and is situated 16 mm. vertically above the alveolar border. Immediately above the infra-orbital foramen, a small portion of the lower margin of the orbit is preserved. The anterior margin of the base of the zygomatic process is situated above the second deciduous molar. The palate is relatively flat and narrow. Its total width between the inner margins of the first permanent molars is estimated to be 16·8 mm., and between the first deciduous molars 18·8 mm. In the young chimpanzee palate shown in text-fig. 15B, the corresponding measurements are 31 mm. and 33 mm. On the other hand, the length of the palate, taken from the level of the posterior border of the first permanent molar is practically the same in the chimpanzee and the fossil specimen. The incisive fossa and the greater palatine foramen show no unusual features. On the upper surface of the palate in the mid-line the groove for the accommodation of the lower border of the vomer is preserved.

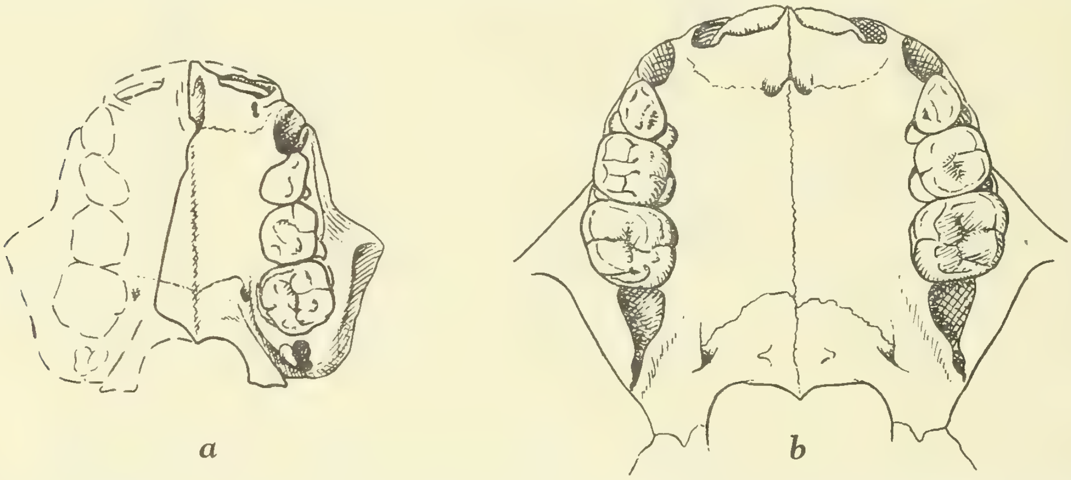

Fig. 15. A. Palatal aspect of the left maxilla of an immature specimen of *P. nyanzae* (993, 1947), compared with

B. The palate of a young chimpanzee of equivalent dental age. Natural size.

In its general proportions, this immature maxilla is clearly somewhat smaller than that of a chimpanzee of corresponding dental age (see text-figs. 14, 15), the subnasal prognathism is less pronounced, the palate is conpsicuously narrower, and the incisor region of the alveolar border is relatively reduced. These contrasts are also apparent when comparison is made with immature skulls of the gorilla and orang. On the other hand, they are such as might be inferred from a consideration of the size and proportions of the teeth and jaws of the mature specimens of *P. nyanzae*.

*C.M.H.*117 (*Rs.*).—Fragment of incisor region of immature maxilla with the crown of an unerupted median incisor partly exposed on a fractured surface. Probably referable to *P. nyanzae* on the basis of general dimensions.

*C.M.H.*116 (*Rs.*).—Fragment of left maxilla with $P\underline{4}$ in position, and the two lateral roots exposed by a fracture. Probably this specimen is referable to *P. nyanzae*, though the premolar crown is rather less compressed antero-posteriorly than in the other specimens, and the internal cingulum is unusually well marked.

*S.*111.—A fragment of the left maxilla containing the much worn crown of the posterior premolar and the roots of the canine and anterior premolar. The dimensions of the teeth and of the maxillary fragment accord very closely with those in the maxilla of specimen C.M.H.2.

*C.M.H.*109 (*R.*106).—A small fragment, much weathered, of the left side of the mandible with the roots of the lateral incisor, canine, and anterior premolar. The specimen is provisionally referred to *P. nyanzae* entirely on the estimated size of the teeth.

*S.*52, 1948.—A fragment of the right maxilla containing the much worn premolar teeth and the first molar. It is difficult to be certain of the identification of this specimen, but the proportions of the teeth conform quite closely to those of specimen C.M.H.2.

Isolated Teeth Attributable to *P. nyanzae*.—In addition to the isolated teeth already described, a number of others (listed below) have been recovered from the East African Miocene deposits. Some of these, particularly the well-preserved lower molars, can be assigned to *P. nyanzae* with confidence. Others, including those which have been exposed to severe wear or weathering, are provisionally assigned to this species on the basis of their general size and proportions.

Incisors

C.M.H.46	Left $I\,\overline{2}$ (unerupted).
C.M.H.21	Right $I\,\overline{2}$ (unerupted).
C.M.H.130 (R.101)	Left $I\,\overline{2}$.
C.M.H.47 (S.)	Left $I\,\overline{2}$.
C.M.H.131 (R.)	Right $I\,\overline{2}$.

Canines

142 (Kathwanga)	Left upper canine (broken).
C.M.H.13 (R.A.1)	Right upper canine.
C.M.H.124 (R.106)	Left upper canine (broken).
C.M.H.123 (R.81)	Right upper canine (tip broken).
843 (Kathwanga)	Right upper canine (broken).
S.45, 1947	Left upper canine.
C.M.H.15 (R.)	Left upper canine (badly weathered).
C.M.H.14 (S.19)	Right lower canine.
C.M.H.17 (R.)	Left upper canine (broken).
C.M.H.16 (R.)	Left upper canine (broken and much worn).
684, 1947 (R.106)	Right lower canine (broken).
C.M.H.118 (R.1)	Right lower canine. This tooth, found in 1947, belongs to the 1942 mandible.
S.53, 1948	Left upper canine.

Premolars

603 (R.106)	Left P $\overline{3}$ (unerupted).
144 (Kathwanga)	Left P $\overline{3}$ (severely weathered).
C.M.H.132 (R.A.1)	Right P $\overline{4}$ (severely weathered).
C.M.H.119 (R.)	Right P $\overline{3}$ and P $\overline{4}$ (embedded together in alveolar fragment).
C.M.H.120 (R.)	Left P $\underline{4}$.
C.M.H.133 (R.)	Right P $\underline{4}$.
C.M.H.23 (R.)	Left P $\underline{4}$.
C.M.H.134 (R.)	Left P $\underline{4}$.

Lower molars

C.M.H.31 (R.)	Right M $\overline{2}$ (unerupted).
143, 1947 (Kathwanga)	Right M $\overline{3}$ (Pl. 5, fig. 31).
C.M.H.135 (R.112)	Right M $\overline{2}$ (Pl. 5, fig. 30).
683, 1947 (R.106)	Right M $\overline{1}$ (Pl. 5, fig. 29).
C.M.H.29 (KB–A)	Left M $\overline{2}$ (severely worn).
1043 (R.113)	Left M $\overline{1}$.
C.M.H.30 (Rs.33)	Right M $\overline{2}$ (much weathered).
1228 (Kathwanga)	Right M $\overline{1}$ (severely worn).
C.M.H.136 (R.A.1)	Right M $\overline{3}$ (weathered).
1229 (Kathwanga)	Left M $\overline{1}$.
C.M.H.137 (R.7)	Left M $\overline{1}$.
R.3, 258	Left dM $\overline{2}$. This tooth is almost a replica of the corresponding tooth in the juvenile mandible (T.265) found at Loperot by the University of California Expedition and now being studied by Dr. W. K. Gregory. Our own specimen is badly weathered and a portion of the enamel has flaked off.
S.58, 1948	Left dM $\overline{2}$. This tooth is somewhat larger than the previous specimen and is better preserved. It is, however, partly damaged by weathering. There is a very pronounced external cingulum which shows secondary beading.

Upper molar

S.112, 1948	Left M $\underline{3}$ (much worn).

The Relation of *P. africanus* to *P. nyanzae.*—Apart from the absolute dimensions of the teeth of the premolar-molar series (Tables 3, 4, and 5) other features of the dentition which distinguish *P. africanus* from *P. nyanzae* are as follows: the greater M $\underline{1}$/M $\underline{2}$ and M $\underline{2}$/M 3 ratios, the marked regression of M $\underline{3}$, the relatively smaller and more slender canines, the tendency to "caniniform" development of the buccal cusp of P $\underline{3}$, the relative height in the upper molars of the internal cingulum which tends to form a projecting shelf, the better definition of the trigon by clear-cut crests joining the protocone, paracone and metacone, the greater tendency for the hypocone to merge broadly with the internal cingulum (in M $\underline{1}$ and M $\underline{2}$), the relatively large size of the hypocone which in the first two molars approximates to that of the protocone, the weak development of the protoconule which forms little more than a slight thickening at the forward angulation of the ridge joining the protocone and metacone, the broader anterior cingulum, the weaker definition of the posterior cingulum, and the absence of the elaborate degree of coarse beading of the internal cingulum which appears to be so characteristic of *P. nyanzae.*

Some systematists may argue that the characters enumerated above, together with the strong contrast in the size and proportions of the mandible, are sufficient to demand a generic distinction. However, we are of the opinion that this would not be justifiable on the material at present available. The diagnostic characters of the teeth which distinguish *P. africanus* from *P. nyanzae* show some degree of individual variability and are difficult to express quantitatively. Some of these differences, also, involve details of the cusp pattern which should not be allowed to obscure the fact that the latter, in its fundamental plan, is similar in the two species. For example, they agree in the strong development of an internal cingulum in the upper molars, in the relative sizes of the cusps in the lower molars and the presence of an external cingulum on the latter, in the morphology of the symphysial region of the mandible and so forth. Moreover, in their absolute dimensions the premolar-molar series in the individual *P. nyanzae* represented by the 1942 mandible and the maxillary fragment 712, 1947, tend to narrow what would otherwise be a marked hiatus separating the species from *P. africanus,* even though the size and proportions of the mandible distinguish them sharply. Pending the discovery of more material, we suppose the smaller dimensions of the dentition in these specimens, as compared with other specimens of *P. nyanzae,* to represent sexual differences in this species, whereas the differences which have been noted between the dentition of the holotype and that of the skull (R.1948, 50) of *P. africanus* appear to represent sexual characters in that species.

TABLE 4

PROCONSUL NYANZAE

Upper Dentition

	P $\underline{3}$			P $\underline{4}$			M $\underline{1}$			M $\underline{2}$			M $\underline{3}$			M $\underline{1}$/ M $\underline{2}$	M $\underline{2}$/ M $\underline{3}$
	a.p.	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*a.p.*
Holotype C.M.H.2	8·0	11·0	137	6·5	11·3	173	9·0	11·5	128	12·0	13·0	108	11·0	14·0	127	75	109
R.1948, 50 . .	8·0	10·5	131	7·0	10·3	147	9·8	11·0	112	12·2	13·5	111	11·3	13·8	122	80	108
C.M.H.33 . .													12·2	14·4	118		
C.M.H.32 . .										10·8	12·0	111					
712, 1947 . .	7·0	10·4	149	5·4	10·9	202	8·4	10·8	128	10·0	11·5	115	9·8	12·4	127	84	102
F.9 . . .										10·7	12·1	113					
C.M.H.21 . .							9·4	11·4	121								
C.M.H.34 . .										11·9	13·6	114					
993, 1947 . .										10·2	11·8	116					

Table 5

PROCONSUL NYANZAE

Lower Dentition

	P $\overline{3}$			P $\overline{4}$			M $\overline{1}$			M $\overline{2}$			M $\overline{3}$			M $\overline{1}$/M $\overline{2}$	M $\overline{2}$/M $\overline{3}$
	a.p.	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*a.p.*
1942 mandible .	8·9	6·6	74	8·5	6·5	76	8·7	8·0	92	10·6	9·3	88	12·0	9·4	78	82	88
603, 1947 . .	10·6	6·5	61														
143, 1947 . .													14·6	11·5	79		
C.M.H.4 . .	10·0	7·0	70	8·0	8·0	100	10·0	8·5	85	13·0	11·0	84	14·0	12·0	85	77	93
M.14086 (B.M.N.H.)	12·6	7·3	58	7·4	8·9	120	9·5	9·5	100	11·4	10·8	95				83	
C.M.H.5 . .				6·6	6·3	96	8·9	7·8	88	11·3	9·5	84				79	
C.M.H.110 . .				8·0	6·8	85	8·2 (est)	7·5	91	11·2	9·5	85				73	
600, 1947 . .				6·7	7·4	91	9·3	8·3	89								
1229 . . .							9·8	8·5	87								
1043 . . .							9·1	7·8	86								
683, 1947 . .							9·4	8·0	85								
C.M.H.31 . .										12·6	10·2	81					
C.M.H.135 . .										12·6	11·0	87					
C.M.H.136 . .													13·7	11·4	83		
C.M.H.7 . .				7·0	7·6	92	9·8	8·2	84								

Table 6

ANTERO-POSTERIOR MEASUREMENTS OF LOWER MOLARS OF VARIOUS DRYOPITHECINAE

(From Pilgrim, 1915, 1927, and Gregory, Hellman & Lewis, 1938)

	M $\overline{1}$	M $\overline{2}$	M $\overline{3}$	M $\overline{1}$/M $\overline{2}$	M $\overline{2}$/M $\overline{3}$
Sivapithecus sivalensis Lydekker	10·6	11·6	13·7	91	85
Sivapithecus sivalensis Lydekker	11·5	13·3	13·8	86	96
S. indicus Pilgrim . . .	12·4	14·5	15·8	86	92
S. salmontanus Lewis . .	11·0	12·6			87
Sugrivapithecus gregoryi Lewis .	11·1	12·6			88
Ramapithecus brevirostris Lewis	9·1	10·2			89
Dryopithecus fontani Lartet (St. Gaudens)	10·0	12·0	12·5	83	96
Dryopithecus fontani Lartet (Lérida)	10·0	11·0	11·5	91	96
D. punjabicus Pilgrim . .		11·3	12·8		88
D. germanicus Abel . . .	9·5	10·6	13·0	90	82
D. germanicus Abel . . .	11·2	10·0	11·8	89	85

Proconsul major Le Gros Clark & Leakey

(see p. 12 for diagnosis)

During 1947, fragments of massive hominoid mandibles considerably larger than that of *P. nyanzae* were discovered at Songhor. The name *P. major* has been given to this type of early Miocene ape.

Holotype.—Part of the body of the right side of the mandible (S.80, 1947). The posterior premolar and all the molar teeth are in position and show an advanced degree of wear. The roots of P $\overline{3}$ are also present and partly exposed at the fractured anterior margin of the fragment. The lower border of the preserved part of the body is missing. The lower end of the anterior margin of the vertical ramus is present where it extends forwards and downwards on to the body. In the complete mandible, it must have overlapped laterally the posterior half of the last molar tooth. The following is a description of the teeth in this specimen (Pl. 5, figs. 34, 35, and text-figs. 17, 18).

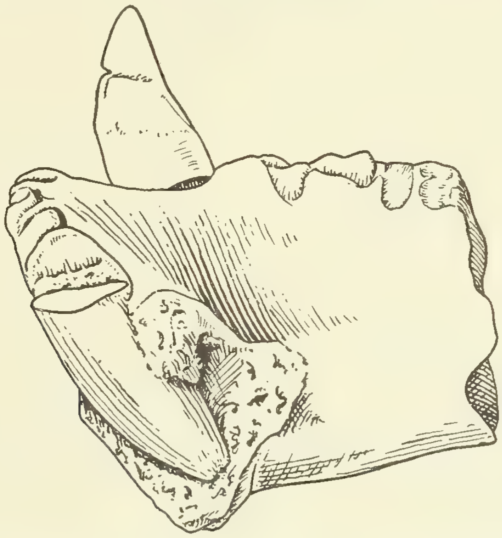

FIG. 16. Symphysial region and part of the right side of the body of a mandible of *P. major* (S.1, 1947) viewed from the medial aspect. The root of the left canine is seen exposed and embedded in the massive symphysis. Natural size.

Dimensions

P $\overline{4}$			M $\overline{1}$			M $\overline{2}$			M $\overline{3}$			M $\overline{1}$/M $\overline{2}$	M $\overline{2}$/M $\overline{3}$
a.p.	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*a.p.*
9·0	9·6	107	11·7	10·3	88	14·4*	12·0	83	17·5	12·6	72	81	82

* Estimated.

P $\overline{3}$.—The roots are set obliquely at an angle of approximately 45° with the axis of the tooth series behind. The tip of the antero-external root is situated at a depth of about 20 mm. below the free margin of the alveolar border.

P $\overline{4}$.—The buccal and lingual cusps of the main part of the crown have been worn down practically level with the talonid basin, leaving a broad area of dentine exposed. The talonid is well marked, and considerably worn. This tooth has three roots, two buccal and one lingual.

M $\overline{1}$.—The crown is approximately rectangular, but slightly broader in its posterior half. The transverse diameter of the trigonid is 9·8 mm., and of the talonid 10·3 mm. All the main cusps are worn down with exposure of islets of dentine. Probably the entoconid was relatively larger than in the corresponding tooth of *P. nyanzae*. The hypoconulid is centrally situated. There is a small trace of an external cingulum in the interval between the protoconid and hypoconid, and antero-externally at the base of the protoconid.

M $\overline{2}$.—The enamel on the posterior surface, and at the postero-external angle, has been broken off. The main cusps have been worn down with exposure of the dentine, but the cusp pattern as well as the general proportions of the unworn tooth were evidently very similar to M $\overline{2}$ in *P. nyanzae*. There is a small remnant of the external cingulum at the antero-external angle of the tooth and opposite the interval between the protoconid and hypoconid.

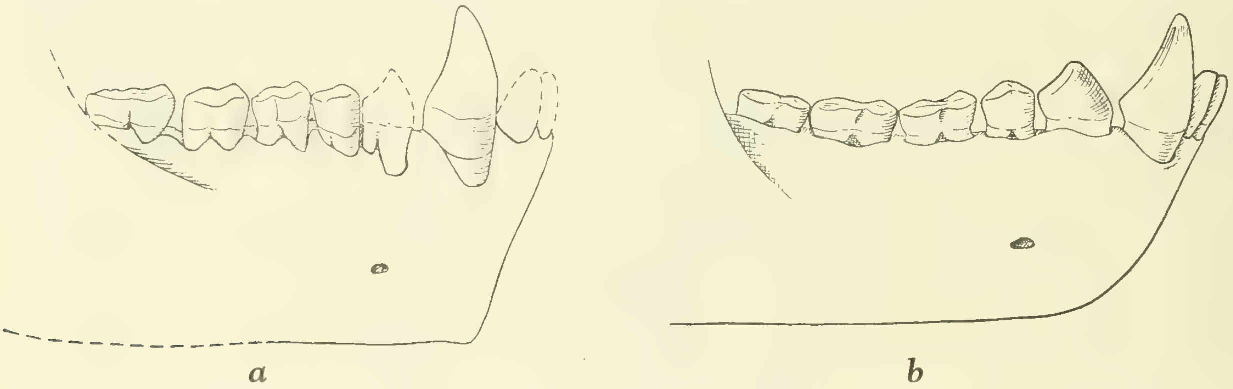

FIG. 17. A. Graphic reconstruction of the right side of the body of the mandible of *P. major* (based on specimens S.1, 1947 and S.80, 1947), compared with
B. The body of the mandible of a male gorilla. $\times \frac{2}{3}$. Note the straight contour of the symphysis in *P. major*, and the vertical implantation of the canine.

M $\overline{3}$.—A large tooth notable for its length (index 72) and for the relative narrowness of the talonid. The cusp pattern is almost entirely obscured by attrition, but in the unworn tooth it was probably similar to that of the last molar of *P. nyanzae*. A trace of the external cingulum remains at the antero-external angle of the tooth—elsewhere it may have been obliterated by wear. The medial and posterior margins of the crown show some irregular crenation produced by the worn remnants of secondary cuspules.

In this specimen the presence of a circular groove of defective enamel formation on P $\overline{4}$ and M $\overline{2}$ (and to a lesser extent on M $\overline{3}$), suggests a dietary deficiency in the corresponding period of dental growth. In the mandibular fragment, the inferior dental foramen is preserved, and its centre is situated 17 mm. behind the posterior surface of the last molar. Below and behind the foramen is seen the groove for the mylohyoid nerve.

S.1, 1947.—The symphysial region and front half of the body of the right side of a mandible (Pl. 5, figs. 36, 37; text-fig. 16). The right canine is complete. The main portion of the crown of the canine was found in 1932, the mandibular fragment containing the base of the crown in 1947, and the tip of the canine in 1948. The portions of the canine fit each other quite accurately. The roots of the incisors, left canine, and right premolars and first molar are embedded in their alveoli, the crowns of all these teeth having been lost.

The lower canine is a massive tooth, with a total length of 57 mm. The height of the crown above the alveolar margin is 24 mm. An inconspicuous internal cingulum is evident on the right canine, and on the posterior aspect of the base of the crown is a strongly marked facet made by contact with the upper canine. On the anterior surface, the lower end of a vertical furrow can be seen. The antero-posterior diameter of the base of the crown is 15·2 mm., and the labio-lingual width 11·0 mm. The roots of the incisors are laterally compressed, and have the following measurements:

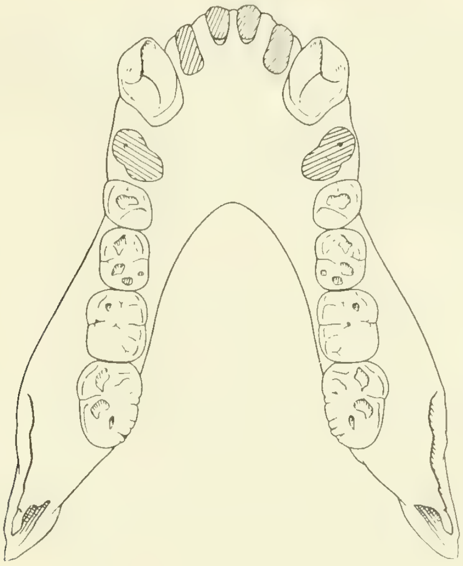

FIG. 18. Graphic reconstruction of the body of the mandible of *P. major*, viewed from the occlusal aspect of the teeth (based on specimens S.1, 1947 and S.80, 1947). × $\frac{2}{3}$. The incisor teeth and the anterior premolars are represented only by their sockets.

	a.p.	*tr.*
I $\bar{1}$	7·2 mm.	4·0 mm.
I $\bar{2}$	9·2 ,,	4·4 ,,

The roots of the two premolar and first molar teeth correspond closely in their dimensions with those of the type specimen. There is a small diastema of approximately 3 mm. between the canine and anterior premolar. The roots of the canine teeth converge towards their tips, the latter being separated by an interval of not more than 16 mm. They are embedded in an exceptionally massive symphysis (text-fig. 16).

The symphysis of the mandible measures 52 mm. along the anterior aspect of its median axis, and its anterior border makes an angle of about 65° with the horizontal lower border of the body. It is marked in front by traces of the line of union between the two halves of the mandible. At the lower border of the symphysis is a small median ridge marking the attachment of the median raphe of the mylohyoid muscle, and on either side of this is a faint digastric impression.

The massive nature of the symphysis is shown in text-fig. 16. Its maximum antero-posterior thickness is approximately 28 mm. On its posterior aspect it slopes downwards and backwards gradually to its most posterior projection, and then slopes abruptly forwards to the lower border. The vertical height of the body of the mandible at the level of the first molar tooth is about 38 mm. The mental foramen is 15 mm. from the inferior border and is situated opposite the posterior border of the anterior premolar tooth. There is no simian shelf.

In text-fig. 17 a reconstruction of the body of the mandible and lower dentition of *P. major,* based on the holotype and specimen S.1, 1947 of this species, is compared with those of a male gorilla. This comparison emphasizes the massive build of the mandible in the fossil specimen, the proportions of the teeth, the vertical implantation of the large canine, and relative straightness in profile of the symphysis. A reconstruction of the mandible as seen from above (text-fig. 18) has been effected by ascertaining the mid-line in specimen S.1, 1947, and reproducing the left side symmetrically. It will be observed that the tooth rows do not diverge posteriorly to any marked degree. The figure emphasizes the relatively small size of the first molar (a characteristic feature also of the other species of *Proconsul*) and the large size of the last molar. Lastly, a comparison with the illustration of the occlusal aspect of the 1942 mandible in text-fig. 9A, and also the series of contours in text-fig. 28, make clear the strong contrast in absolute dimensions between *P. nyanzae* and *P. major.*

*C.M.H.*142 (*R.*106).—This mandibular fragment from Rusinga is provisionally allocated to *P. major* because of its general dimensions. It consists of the anterior extremity of the body of the right side of the mandible with the roots of the canine and two premolar teeth in position, and the anterior root of the first molar. The root of the canine measures 14·0 mm. in its maximum (labio-lingual) diameter, and the tooth was evidently a powerful one. The diameters of the roots of the premolar teeth are slightly less than those of the other specimens. The vertical height of the body of the mandible at the level of the first molar tooth is estimated at 38 mm. In four specimens of *P. nyanzae* this measurement was found to have a range of 30–35 mm. By itself this fragment does not add further information.

*S.*55, 1948 (Pl. 6, fig. 38).—This crown of an unerupted left lower molar conforms in its relative proportions and cusp pattern to a second molar of *P. nyanzae,* but it is very much larger, and is even larger than the corresponding tooth in the holotype of *P. major.* Its dimensions are as follows:

a.p.	*trans.*	*index*
15·6 mm.	14·0 mm.	90

The enamel has been subjected to weathering, and the measurements recorded above are therefore assumed to need some correction. The cusp pattern is very similar to that of M $\overline{2}$ in *P. nyanzae.* The protoconid is somewhat larger than the metaconid.

In front of these cusps is a well-marked fovea bounded anteriorly by a crinkled cingular ridge. The hypoconulid is well developed and its apex occupies a position approximately in the median axis of the crown. The surfaces of the cusps forming the talonid basin are finely wrinkled, and there is also coarse wrinkling, much accentuated by weathering, of the buccal surface of the hypoconid. A distinct posterior fovea is present. Traces of an external cingulum are found at the base of the metaconid and at the interval between the latter and the base of the hypoconid.

S.56, 1948 (Pl. 6, fig. 39).—A posterior left lower premolar slightly worn and weathered. It is somewhat larger than $P\overline{4}$ of the holotype of *P. major*.

a.p.	*tr.*	*index*
8·9 mm.	10·6 mm.	119

The two main cusps are of approximately equal size, and are separated by an antero-posterior sulcus which terminates in front in a small fovea. The talonid forms a relatively large part of the crown, and is prolonged back slightly at its postero-internal angle to support a small but distinct entoconid.

*C.M.H.*35 (*S*) (Pl. 6, fig. 40).—A second (?) right upper molar tooth (probably recently erupted) from Songhor. Because of its large size, it is here provisionally assigned to *P. major*. The dimensions of this tooth are as follows:

a.p.	*tr.*	*index*
12·7 mm.	15·3 mm.	120

As in all upper molar teeth of the genus *Proconsul*, the trigon forms a relatively small proportion of the whole crown. The three main cusps are pyramidal with a broad base, and they are of approximately equal size. The protocone is connected with the paracone and metacone by clear-cut crests, and a ridge also extends laterally from its tip to become continuous with the anterior cingulum. The hypocone is somewhat smaller than the protocone. It is connected with the base of the metacone by a low ridge behind which is a well-developed posterior fovea. From the lingual cusps, the inner surface of the crown slopes with a pronounced medial inclination towards the base. The internal cingulum is very strongly developed, with an elaborate beading. From the latter a series of fine parallel ridges extends along the medial side of the protocone and the anterior aspect of the hypocone. A remnant of the external cingulum is present at the interval between the bases of the paracone and metacone. The anterior and posterior cingula are also conspicuously developed. The lateral roots of this tooth are missing, but the medial root is present except for the tip, and diverges medially very strongly.

Relationship of *P. major*.—The outstanding feature of this species is the great size of the teeth and mandible, and it is on this character that a specific distinction from *P. nyanzae* appears to be justified. The comparisons which have already been pointed out in the description of the material serve to emphasize the contrast. The few specimens so far available do not, of course, give any indication of the range of variation in size in *P. major*, and further material may show that the contrast with *P. nyanzae* is not so marked as now appears to be the case. Nevertheless, it would be difficult to allocate them to the same species, particularly since we have already noted a considerable range of variation in size (perhaps sexual) within the limits of the species *P. nyanzae*.

Comparisons with fossil apes found elsewhere show that the only type which may exceed *P. major* in size is *Dryopithecus giganteus* (Pilgrim, 1915), but this species is known only by a third lower molar tooth from the Siwalik formations.* According to Pilgrim (1915) the antero-posterior diameter of the tooth is 19·1 mm. and the transverse 15·3 mm. *Sivapithecus indicus* appears to be the next largest representative of the Indian Dryopithecinae, and the absolute dimensions of the teeth (except those of M $\overline{3}$) approximate to those of *P. major*. The measurements in this species are recorded here for comparison.

TABLE 7

MEASUREMENTS OF LOWER MOLARS OF *SIVAPITHECUS INDICUS* Pilgrim

	M $\overline{1}$			M $\overline{2}$			M $\overline{3}$			M $\overline{1}$/M $\overline{2}$	M $\overline{2}$/M $\overline{3}$
	a.p.	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*a.p.*
Ind. Mus. D.176 (Pilgrim)							14·3	13·4	94		
Ind. Mus. D.177 (Pilgrim)	11·5	10·6	92	13·0	12·3	95				88	
Y.P.M.13828 (Gregory, Hellman & Lewis)	12·4	11·8	95	14·5	13·7	94	15·8	13·6	86	86	91
611 (Gregory, Hellman & Lewis)							15·0	12·0			

S. indicus differs pronouncedly in the breadth index of the lower molars, in the length of the last molar, and in the ratio of the lengths of the molars to each other. The relatively small size of the first molar in *P. major* is a distinguishing feature wherein it shows its affinities with the other species of *Proconsul* from the early Miocene of East Africa.

Sivapithecus africanus Le Gros Clark & Leakey

(see p. 13 for diagnosis)

The upper molar teeth in the genus *Proconsul* are characterized in all species by a strong development of the internal cingulum. The Miocene deposits of the same area in Kenya have also yielded a maxillary fragment with P $\underline{3}$, P $\underline{4}$, and M $\underline{1}$, and two isolated upper molars, in which the molar pattern is quite different, the internal cingulum being almost entirely absent and the crown structure relatively very simple. The premolars are more massive than in *P. nyanzae* and the first molar is larger in absolute dimensions and has a lower breadth index. Direct comparison with casts, stereo-photographs, and drawings of the few dryopithecine maxillary teeth which are available from Europe and Asia shows that they are very similar to those, and in details of proportions and cusp pattern they resemble *Sivapithecus* so closely that they must be provisionally assigned to this genus. In a few minor characters, however, they show certain distinctive features which may have a specific value; hence we have suggested that these East African specimens should be assigned to a new species, *S. africanus.*

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* Remane (1921) maintains that this tooth is a second molar, in spite of the fact that it shows no pressure facet on its posterior aspect. The excellent illustration which Pilgrim gives in his report seems to support his own diagnosis.

The holotype of this species is the maxillary fragment (C.M.H.6) which was found on Rusinga Island and figured by MacInnes (1943). The following is a description of this specimen.

*Maxillary fragment C.M.H.*6 (*R.*106) (Pl. 6, figs. 41, 42, 43).—A small fragment of the left maxilla with the base of the lower border of the zygomatic process, a narrow portion of the palatal surface, the two premolars and first molar excellently preserved, and the roots of the second molar. The anterior premolar is a relatively massive tooth characterized by an unusual width. The labial cusp is considerably larger than the lingual, and projects down to a lower level, though not to the extent seen in *P. africanus.* From its apex well-defined crests extend to the anterior and posterior borders of the crown, the former being longer than the latter. The two cusps are not interconnected by a central transverse crest but are well separated by a deep antero-posterior sulcus. A well-marked anterior cingulum and a distinct posterior cingulum are present. The anterior margin of the crown is conspicuously concave, presumably in relation to a somewhat stout canine. The anterior premolar has two lateral roots which diverge markedly from each other. In $P\underline{4}$ the two cusps are sub-equal. Anterior and posterior cingula are well developed, the latter being continued forward on to the medial aspect of the crown to form a distinct internal cingulum. The two cusps are not interconnected in the centre of the crown. In the first molar, the trigon is well defined, the protocone being connected with the paracone and metacone by clear-cut crests. As a result of a convergence of the main cusps, the trigon basin is relatively small in relation to the size of the crown as a whole. The protocone has the largest base of the three cusps of the trigon; it is equalled in size by the hypocone. The latter is sharply separated from the trigon by a continuous sulcus. There is a very small anterior fovea, and a trace of the antero-internal cingulum. A shallow posterior fovea marked by fine secondary crenations is bounded behind by a low posterior cingulum. The internal cingulum is absent (except for a trace antero-internally) and there is no trace of an external cingulum. Judging from the roots of the second molar, this tooth was not conspicuously larger than the first.

Since a part of the intermaxillary suture is preserved on the palatal process it is possible to estimate the width of the palate between the inner margins of the first molars. This could not have exceeded 20 mm., indicating that the palate was rather narrow in comparison with the size of the premolar and molar teeth. In the specimen of the maxilla of *P. nyanzae* (C.M.H.2), the corresponding palatal width is over 30 mm., though the premolar and molar teeth are actually smaller.*

*C.M.H.*26 (Pl. 6, fig. 44).—An unerupted first right upper molar, found in the

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* From a cast of the palate and dentition of *Sivapithecus sivalensis* reconstructed by Gregory, Hellman & Lewis (1938), it is estimated that the width of the palate between the first molars in this species was about 25 mm.

Miocene deposits of Maboko Island. Its absolute dimensions are practically the same as those of the M $\underline{1}$ of C.M.H.6, and it is even simpler in its cusp pattern. The trigon is very well defined; the protocone is slightly larger than the paracone and metacone, which are of approximately equal size. The hypocone is clearly demarcated and somewhat smaller than the protocone. Small anterior and posterior foveae are present, and there is a trace of an antero-internal cingulum. As in the holotype, internal and external cingula are otherwise absent.

C.M.H.27 (Pl. 6, fig. 45).—A right upper second molar tooth from an unknown locality in the Kavirondo area. The trigon is less well defined and less regular than in the first molar. The protocone is about equal in size with the paracone, but the metacone is much smaller. The hypocone is also relatively small, so that the posterior half of the crown is distinctly narrower than the anterior half. The backward protrusion of the hypocone tends to give a rhomboidal shape to the occlusal surface.

The crests connecting the protocone with the paracone and metacone are low and rounded and the trigon basin relatively shallow. A narrow anterior fovea is bounded in front by a low anterior cingulum which, at its inner extremity at the base of the anterior margin of the protocone, is raised into a small but prominent rounded cuspule, the protoconule. There is a well-marked posterior fovea. Neither the internal nor the external cingulum is developed.

Comparison of *S. africanus* with other Dryopithecinae.—Unfortunately few upper molars of *Dryopithecus* are available for comparison. The first upper molar of *D. darwini* from the middle Miocene of the Vienna basin, discovered in 1931 by Glaessner, is considerably worn. The trigon is relatively larger than in *S. africanus*, and the paracone is relatively more massive. Moreover, the hypocone (so far as can be judged by photographs) is not so sharply separated from the protocone. The second upper molars of *D. germanicus* (Branco, 1898) are smaller and have a higher breadth index. The crown is also complicated by a number of secondary furrows. The paracone is relatively large and the posterior fovea is pronounced. The hypocone has no backward projection as in *S. africanus*, and is not so completely separated from the metacone. The maxillary fragment of *D. punjabicus* described by Pilgrim (1915) provides a more useful comparison with *Sivapithecus*, for it contains the two premolars and the first and second molars. The premolars are much smaller than those of *S. africanus* in absolute dimensions (particularly in width) and also relatively to the first molar. They appear to lack the deep and clear-cut antero-posterior furrow separating the labial and lingual cusps, the latter being connected by strong ridges across the centre of the crown. No mention is made by Pilgrim, in his detailed description, of an internal cingulum on the first premolar. The first molar is almost the same size as that of *S. africanus*, but it differs in the much larger size of the trigon, in the more conspicuous and deeper anterior and posterior foveae, in the relatively large size of the paracone, and in the fact that the hypocone is connected by a strong ridge with the metacone. The second molar has a higher breadth index than that of *S. africanus*, and in this tooth the paracone is relatively larger as compared with the protocone, and the hypocone is much smaller and does not project backwards to any marked extent.

The upper molars of *S. africanus* thus resemble those of the genus *Dryopithecus* in size and general proportions, but differ significantly in the proportionate development of the cusps, in the development of the posterior fovea, and in the lesser degree of secondary folding of the enamel. Further, the premolars of *Dryopithecus* are significantly smaller and show pronounced differences in the cusp pattern. If a comparison is now made with the Indian species of *Sivapithecus*, the resemblance is found to be much closer; indeed, the morphological similarities are so complete as to make it impossible to separate the Kenya specimens generically on the basis of the limited material available. Pilgrim (1927) described in detail the upper dentition of *S. orientalis* preserved in the left maxilla found in the Nagri horizon of the Siwalik formations (Lower Pliocene), and also an isolated first upper molar of *S. indicus* from the Salt Range. The upper dentition of another species (*S. sivalensis*) from the Nagri zone has been described by Gregory, Hellman & Lewis, as well as isolated upper teeth of *S. indicus* from the Chinji, Nagri, and Kamlial zones. P $\underline{3}$ of the Siwalik fossils resembles that of *S. africanus* in its dimensions, the strongly developed anterior cingulum, the contour of the anterior margin of the crown, the relative size of the two main cusps and the separation of the latter by a well-defined antero-posterior sulcus. According to Pilgrim (1927), the first upper premolar has a single external root, "thus differing from *Dryopithecus* and *Palaeopithecus*". In *S. africanus* it has two. But in this connection, it should be noted that *Palaeopithecus* has now been referred by Lewis (1937) to *Sivapithecus* (*vide infra*). P $\underline{4}$ is similar in its dimensions and cusp pattern, but no mention of an internal cingulum is made in the description. The first molar is of closely comparable size but has a slightly higher breadth index. The characteristic features displayed by the relative massiveness of the protocone base, the relatively small and clear-cut trigon, the small anterior and posterior foveae and the sharply demarcated hypocone, as well as by the general simplicity of the crown so far as gross secondary foldings of the enamel are concerned, are all exactly paralleled in *S. africanus*. In an isolated first upper molar of "*Sivapithecus cf. indicus*" described by Gregory, Hellman & Lewis, they note that an incipient Carabelli cusp is present, which with the general configuration of the main cusps gives the tooth "a curiously sub-human look". M $\underline{2}$ is characterized, as in the African species, by the still more massive relative size of the protocone, the reduced metacone, and a backward projection of the hypocone which gives a rhomboid shape to the occlusal aspect of the crown. Unlike *Dryopithecus*, also, the enamel is relatively free from secondary foldings and the hypocone is sharply separated from the protocone and metacone by a clear-cut sulcus. The development of a secondary cuspule (protoconule) at the base of the anterior margin of the protocone is another curious point of similarity. The cuspule is particularly well marked in the isolated second molar referred to *S. africanus* (C.M.H.27). Schlosser (1901) noted a similar cuspule in one of the upper molars of *D. germanicus*, but in this specimen it appears to be much less pronounced than in M $\underline{2}$ of *S. orientalis* and *S. africanus*. The anterior and posterior foveae of both these species are almost identical in their degree of development. In their study of fossil apes from India, Gregory, Hellman & Lewis list the characters in which the upper molar of *D. germanicus* differs from that of *S. sivalensis*. We find ourselves in agreement with most of these distinctions, though some appear to be of more importance than others. Clearly the upper molars of *Dryopithecus* and of *Sivapithecus* contrast rather strongly—more so, indeed, than the lower molars. The characteristic features of the upper molars of *Sivapithecus* are as follows:

(1) They are larger in general dimensions than those of *Dryopithecus*.
(2) The cusps are of regular pyramidal shape, with a broad base which gives them a massive appearance. In *Dryopithecus*, they are more delicately constructed.
(3) The outer and inner cusps are markedly convergent, so that the trigon basin is relatively constricted in relation to the size of the crown as a whole. The trigon has a regular compact appearance, being bounded by very well-defined crests. In *Dryopithecus*, the trigon is relatively larger since the main cusps are more splayed apart.
(4) The base of the hypocone (particularly in M $\underline{2}$) protrudes backwards more than in *Dryopithecus*.
(5) The paracone and metacone are sub-equal, whereas in *Dryopithecus* the paracone is relatively larger.
(6) The enamel is singularly free from coarse secondary foldings. In *Dryopithecus*, these are more strongly developed.
(7) The hypocone is sharply separated by a continuous sulcus from the protocone and metacone, whereas in *Dryopithecus* it is connected with the metacone by a broad ridge, and is also less distinctly marked off from the base of the protocone.
(8) The posterior fovea is very slightly developed. In *Dryopithecus*, it is a conspicuous feature.

The other outstanding feature of *Sivapithecus* in contrast to *Dryopithecus* is the large size of the premolar teeth, as shown particularly in their transverse diameter, and in their size relative to the molars.

In most of the characters enumerated above, it seems clear that *Sivapithecus* is almost certainly more primitive and generalized than *Dryopithecus* (contrary to the conclusions expressed by Gregory, Hellman & Lewis, 1938). The relatively small, compact and sharply outlined trigon (formed by cusps of approximately equal size) is not only characteristic of early Primates as a whole, it is also a distinctive feature in all the other early Miocene apes from East Africa, as well as in the primitive *Pliopithecus* and in the modern gibbon. In the widening of the trigon and the relative enlargement of the paracone, *Dryopithecus* approaches more closely to the modern African apes. The relative smoothness of the enamel surface in *Sivapithecus*, the clear separation of the hypocone from the trigon, and the slight development of the posterior fovea are likewise to be regarded as primitive characters. These inferences accord with the evidence of the early Miocene material from East Africa that *Sivapithecus* is evidently much more ancient than any remains of the genus *Dryopithecus* hitherto found, and also with the conclusions of previous authorities that the various species of *Dryopithecus* from late Miocene and early Pliocene deposits already show indications of evolutionary development in the direction of the modern orang, chimpanzee, and gorilla.

If we adopt the diagnostic criteria of the genus *Sivapithecus* listed above, *Palaeopithecus* Lydekker should be included in this genus, as Lewis (1937) maintained. It also seems certain that the isolated upper molar (D.187) referred by Pilgrim (1915) to *D. punjabicus* is really a *Sivapithecus* molar.

The question naturally arises whether any of the isolated lower molars found in the Kavirondo area that have been provisionally ascribed to *Proconsul* are in fact attributable to *Sivapithecus*. However, in all these teeth, the rather strong development of the antero-external cingulum is a distinctive feature which does not appear to be present in the Indian forms of this genus. In the Siwalik specimens, the first molar is small compared with the second, but not so small as in the Kenya material so far available.

In summary, the upper teeth of *S. africanus* differ from those of all the other large apes from the early Miocene deposits of East Africa in the absence of an elaborate internal cingulum and in the relative simplicity of the cusp pattern. They closely resemble the Asiatic species of *Sivapithecus* (and differ from the genus *Dryopithecus*) in the large size of the upper premolars, the relative size of the main cusps of the upper molars, the limited extent and sharp definition of the trigon, the absence of coarse secondary foldings of the enamel, the absence of a large posterior fovea, and the clear separation of the hypocone from metacone and protocone. The specific separation of *S. africanus* from the Asiatic types may be justified by certain features such as the flatness of the palate (which Pilgrim notes is high and arched in *S. orientalis*), the persistence of a trace of the antero-internal cingulum on the upper molars (which, however, is also indicated in an upper molar, D.176, of *S. indicus*—Pilgrim, 1927), the development of the internal cingulum on P $\underline{4}$, and the slightly smaller width of the first and second upper molars. Moreover, it is extremely improbable that representatives of an identical species would be found so widely separated in time and space.

Table 8

MEASUREMENTS OF UPPER TEETH OF VARIOUS DRYOPITHECINAE, COMPARED WITH *SIVAPITHECUS AFRICANUS*

(From Pilgrim, 1915, 1927, and Gregory, Hellman & Lewis, 1938)

	P $\underline{3}$			P $\underline{4}$			M $\underline{1}$			M $\underline{2}$		
	a.p.	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*
S. africanus L.G.C. & L. (C.M.H.6)	8·2	12·3	150	7·5	11·8	157	10·6	11·3	107			
S. africanus L.G.C. & L. (C.M.H.26)							10·6	11·1	105			
S. africanus L.G.C. & L. (C.M.H.27)										12·0	11·6	97
S. orientalis Pilgrim (D.196)	7·7	—	—	7·3	12·0	164	11·0	12·0	109	12·8	14·2	111
S. sivalensis (Lydekker) (617 & K.29/466)	8·7	11·0	126	7·6	11·4	150	10·6	12·2	115	11·5	13·7	119
S. sivalensis (Lydekker) (614)							10·3	12·1				
S. indicus Pilgrim (D.176)							10·9	12·7	117			
S. indicus Pilgrim (D.191)							10·5	13·5?	129?	12·5	14·0	112
S. indicus Pilgrim (612)							11·3	12·4	109			
S. indicus Pilgrim (613)										12·7	15·5	122
S. indicus Pilgrim (616)	8·9	11·3	127							13·3	15·3	115
Palaeopithecus (?*Sivapithecus*) *sivalensis* Lydekker	6·8	11·4	168	6·8	11·4	168	10·8	12·0	111	11·3	12·9	114
D. punjabicus Pilgrim	7·0	9·5	136	6·6	9·7	147	10·4	11·3	109	10·6	11·4	108
D. germanicus Abel							9·6	10·0	104			
D. germanicus Abel										10·4	11·0	106

Genus *Limnopithecus* Hopwood

Limnopithecus legetet Hopwood

(= *L. evansi* MacInnes)

Hopwood (1933) described the species *Limnopithecus legetet* on the basis of a mandibular fragment containing the first and second permanent molars, and another fragment of a young individual with the two deciduous molars. He showed that in several respects the permanent lower molars display resemblances to *Pliopithecus*. MacInnes (1943) described further specimens of a small anthropoid ape from Songhor, which he assigned to *Limnopithecus*. Of these, the best preserved is the major portion of the right side of the body of a mandible (S.13) containing the premolar-molar series in excellent condition, except P $\overline{3}$ which has lost the front part of the crown. The mandible was evidently of relatively light build, but with a body much deeper than in small varieties of the modern gibbon, and even deeper than in some of the larger siamangs (MacInnes, 1943, pl. 23, figs. 3, 3a). The following measurements recorded by MacInnes have been repeated and confirmed.

Height of body of mandible at level of P $\overline{3}$ . .	17·5 mm.
Height of body of mandible at level of M $\overline{3}$ . .	17 ,,
Thickness of body of mandible at level of M $\overline{1}$.	8 ,,
Length of tooth row P$\overline{4}$–M $\overline{3}$	22 ,,

The details of the cusp pattern of the teeth are as follows (Pl. 6, fig. 46). Most of the crown of the anterior premolar is missing. It is apparent from what is left of the tooth, however, that it was disposed very obliquely in the jaw (at an angle of about 45°). In P $\overline{4}$, there are two main cusps situated close together and joined by a rather sharp transverse ridge. The buccal cusp is slightly the larger. A broad but abbreviated talonid is situated postero-medially. There is a slight indication of an external cingulum. The cusps of the molar teeth are quite distinct in their morphology from those of the various species of *Proconsul*, for whereas in the latter the cusps have a "crystalline" appearance, being of polyhedral shape with flattened sides, in *Limnopithecus* they are more in the form of small rounded conical tubercles. The summits of the tubercles are raised into attenuated points thinly covered by enamel, so that quite early in the wear of the tooth the dentine is exposed here and thus becomes evident as a pattern of small dots on the occlusal surface of the crown (Pl. 6, fig. 46). Further, the cusps are somewhat small relatively to the size of the crown as a whole, and are arranged round the margins of a talonid basin which forms rather a broad shallow cup-like excavation in the centre. In these respects (as well as in size), the lower molars have a striking resemblance to those of the small modern gibbons. They differ, however, in that the conical cusps are more individualized, being clearly demarcated from each other by relatively deep intervening sulci. In *Hylobates*, they tend to be united at the periphery of the talonid basin by interconnecting crests. The enamel in *Limnopithecus* is singularly free from secondary foldings.

In M $\overline{1}$, the protoconid is situated definitely in advance of the metaconid, so that the low crista transversa joining them is directed forwards and laterally, but the crest is not sharply defined. The hypoconid is situated opposite the interval between the metaconid and entoconid. The bases of the metaconid and hypoconid make a broad contact in the centre of the crown. The hypoconulid is relatively large and is situated approximately in the median axis of the crown. There is a small anterior fovea, and a somewhat feebly developed posterior fovea. The external cingulum is well marked antero-externally and postero-externally. The crown of M $\overline{1}$ is rectangular in its occlusal contour, the width of its anterior and posterior moieties being approximately equal. M $\overline{2}$ is larger than M $\overline{1}$, but there is no strong contrast in size as in the genus *Proconsul*. The cusps are arranged as in M $\overline{1}$; the hypoconid is well advanced in front of the level of the entoconid, and the external cingulum is even more pronounced. The hypoconulid is separated from the entoconid by an uninterrupted sulcus. The width of the talonid is slightly less than that of the trigonid. The posterior fovea is small. M $\overline{3}$ has a more elongated crown, narrowing towards the hypoconulid. The latter is median in position and of approximately the same size as the entoconid. There is no definite posterior fovea. The external cingulum is strongly developed. The width of the crown is 5·2 mm. opposite the protoconid, and 4·8 mm. opposite the hypoconid. The general dimensions of the lower premolar and molar teeth of *L. legetet* are given in Table 10.

Other points to be noted about the mandibular fragment S.13 are as follows. At the broken posterior margin, the lower border begins to descend rather abruptly, indicating an extension downwards of the masseteric surface of the ascending ramus. The preservation of the mid-line of the lower border of the symphysis makes it clear that the incisor region must have been relatively narrow. There is no simian shelf. The mental foramen, which is single, is situated at the level of the interval between P $\overline{3}$ and P $\overline{4}$, only slightly below the centre of the body of the mandible. Part of the root of the right lower canine is preserved embedded in its socket; it had a transverse diameter near the alveolar border of about 5 mm.

MacInnes assigned specimen S.13 to Hopwood's species *L. legetet*, but his other specimens he regarded as representing another species, which he called *L. evansi*, distinguished by the slightly larger size of the lower molars, the lower width index of P $\overline{4}$, the relatively narrower molars, and the smaller depth of the body of the mandible. We have examined this material carefully and are able to recognize the differences to which MacInnes draws attention, but we do not feel that they imply a specific distinction. It has become apparent, for example, since Hopwood's original definition of *Limnopithecus*, that the length-breadth index of the lower molars shows considerable individual variation as it does, according to Remane, in each species of *Hylobates*. Although the recognition of *L. evansi* as a separate species may prove to be justified when more complete material is available, for the present it seems desirable to allocate all the smaller specimens of *Limnopithecus* to *L. legetet*, and to extend Hopwood's original diagnosis of this species to include what are possibly only intra-specific variations. In our general discussion of the genus *Limnopithecus*, *L. legetet* has been taken to include also all specimens of *L. evansi* MacInnes. These specimens are:

*C.M.H.*104 (*S.*) (Holotype of *L. evansi* MacInnes, 1943, pl. 23, figs. 4, 4a).—A portion of the right side of the body of a mandible with P $\overline{4}$–M $\overline{3}$. The height of the mandible at the level of M $\overline{1}$ and also at M $\overline{3}$ is 14·5 mm. (as compared with 17–17·5 mm. in the specimen S.13). The proportions of the teeth are somewhat different from those of S.13 (as can be seen by reference to Table 10), but the cusp patterns are essentially similar. The last molar is defective. The anterior fovea is very small in both M $\overline{1}$ and M $\overline{2}$, and the posterior fovea is only represented by a minute depression.

*C.M.H.*105 (*S.*) (Paratype of *L. evansi* MacInnes, 1943, pl. 23, figs. 6, 6a, 6b).—The right side of the body of a mandible with the symphysial region (text-figs. 19, 20). It contains, in a severely weathered condition, P $\overline{4}$–M $\overline{3}$ on the right side, P $\overline{3}$ on the left side, and the roots of the incisors and canines. In addition, the base of the crown of the right canine is partly preserved. Little need be said about the posterior premolar and the molar teeth. They conform very closely indeed to those in the previous specimen in size, proportions, and cusp pattern. The left anterior premolar is excellently preserved. It is of the sectorial type, with a single pointed cusp. From the apex of the cusp well-defined ridges extend down to the anterior and posterior margins of the tooth, and also down the medial aspect to join the internal cingulum. There is a short talonid, and no external cingulum. The crown is laterally compressed and its long axis is disposed obliquely (text-fig. 20). By comparison with *Hylobates*, P $\overline{3}$ in this specimen of *Limnopithecus* is more primitive in the following characters: it is not laterally compressed to such a degree, the talonid is not so prominent, the anterior border of the crown is shorter and the enamel does not extend downwards anteriorly on to the anterior aspect of the lateral root. In brief, the sectorial character of the tooth is less pronounced than in the modern gibbon.

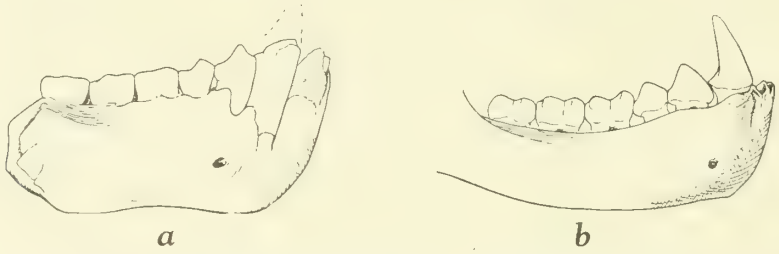

Fig. 19. A. Lateral view of the right side of the body of a mandible of *L. legetet* (C.M.H.105), compared with B. The mandible of a gibbon, *Hylobates mulleri*. Natural size. In the fossil specimen, the stumps of the incisor teeth are obscured by matrix. The outline of the crown of the canine has been indicated by reconstruction and the anterior premolar (which was missing on the right side) has been drawn from that of the left side.

The dimensions of their roots indicate relatively stout canine teeth—the antero-posterior diameter at the level of the alveolar border (measured on the left side where the root is more perfectly preserved) is 6·7 mm., and the transverse diameter 4·7 mm. The dimensions of the upper ends of the roots of the incisors are as follows:

	a.p.	*tr.*
I $\overline{1}$	3·6 mm.	2·0 mm.
I $\overline{2}$	3·8 ,,	2·2 ,,

Compared with the size of the teeth, the body of the mandible is distinctly robust. Some of the dimensions given by MacInnes (1943) are here appended:

Height of the body at level of P $\bar{3}$	18 mm.
Height of the body at level of M $\bar{3}$	15 ,,
Thickness of body at level of M $\bar{1}$	7 ,,
Length of symphysis	22 ,,

In text-figs. 19, 20 are shown outline drawings of specimen C.M.H.105 compared with drawings to the same scale of the mandible of a male *H. mulleri*. From these illustrations it is clear that in the fossil genus the mandible was more solidly constructed than in the modern gibbon, though the cheek teeth are of comparable size. The canine is much stouter in this specimen of *Limnopithecus* and projects more vertically upwards, while the symphysial region is narrower and more pointed.

*C.M.H.*106 (*S.*) (MacInnes, 1943, pl. 23, figs. 5a, 5b).—A fragment of the left side of the body of a mandible with M $\bar{1}$ and M $\bar{2}$ in position. The teeth in this specimen are well worn and slightly larger than in the other specimens of this species. For these reasons their identification is somewhat uncertain—possibly they are referable to *L. macinnesi* (see below). In the first molar the protoconid is placed definitely in advance of the metaconid (Pl. 6, fig. 47). The height of the body of the mandible at the level of M $\bar{3}$ is approximately 16 mm.

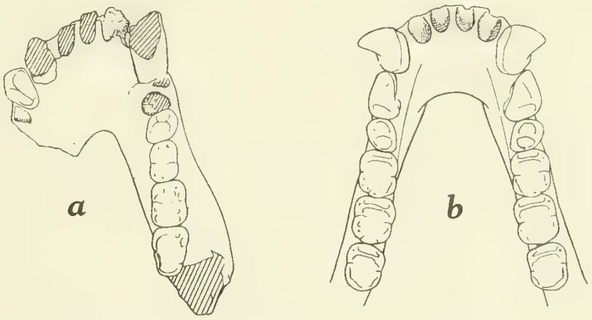

FIG. 20. A. Occlusal aspect of the mandible of *L. legetet* (C.M.H.105), compared with B. The mandible of a gibbon, *Hybolates mulleri*. Natural size.

The following specimens are new; they are fragmentary, and their identity is not in all cases certain.

*C.M.H.*108 (*R.*106).—A small fragment of the alveolar border of the mandible with M $\bar{2}$ and M $\bar{3}$. The teeth are much weathered, and the measurements given in Table 10 are only approximate. Their cusp pattern and proportions are almost identical with those of specimens C.M.H.104 and 105.

*S.*121, 1948.—Fragment of alveolar border of mandible containing the second and third molars in excellent condition and almost unworn. The external cingulum is very pronounced in both teeth. The cusp pattern and proportions of the teeth are similar to those already described, but in absolute size they are somewhat larger than the type specimen C.M.H.104 (Pl. 6, fig. 50). The posterior fovea in M$\bar{2}$ is very small and shallow, and the hypoconulid is an isolated tubercle demarcated from the entoconid by a complete sulcus.

Koru 1, 1948.—Fragment of alveolar border with the right M $\overline{3}$ partly worn. The tooth resembles M $\overline{3}$ in the specimen of *L. legetet* (S.13) very closely, but it is slightly larger. The external cingulum is well developed.

Koru 2, 1948.—Fragment of alveolar border with the left M $\overline{2}$ considerably worn.

944, 1947 (*R. Survey Beacon, No.* 2).—Mandibular fragment with M $\overline{1}$ and M $\overline{2}$. This specimen is too severely weathered to permit detailed study. The height of the body of the mandible at the level of M $\overline{1}$ is estimated to be approximately 13 mm.

S.5.—A mandibular fragment including the symphysial region and adjacent part of the right side of the body. The right first molar is in position and is considerably worn, and the roots of the canine and the two premolars are still embedded in their sockets. The first molar is closely similar to that of C.M.H.104. It is distinctly broader in its posterior moiety. The canine was evidently a small tooth, for the antero-posterior and transverse diameters of the root at the level of the alveolar margin are estimated to be approximately 4·5 mm. and 3·0 mm. The height of the body of the mandible at the level of M $\overline{1}$ is 14 mm., and the length of the symphysis is approximately 15 mm. This specimen is evidently part of a much smaller mandible than specimen C.M.H.105. That it belongs to a fully mature animal is shown by the absence of any indication of unerupted teeth in an X-ray photograph and by the advanced degree of wear of M $\overline{1}$. The small size is perhaps evidence of sexual differentiation.

S.60, 1948.—Symphysial fragment of mandible with the roots of the incisors, canine and anterior premolar embedded in their sockets. The canine is larger than in the previous specimen, the antero-posterior and transverse diameters of its root at the level of the alveolar margin being 5·8 mm. and 4·0 mm. The symphysis is also rather longer—18 mm.

S.409, 1948.—Left side of symphysial region of mandible with the roots of the incisors and premolars, and most of the crown of the canine (except for the tip). The diameters of the canine at the base of the crown are 6·0 mm. and 4·4 mm. The height of the crown above the alveolar margin was probably about 7 mm. The length of the symphysis in the mid-line is 17 mm. The mental foramen is situated at the level of the anterior premolar tooth, approximately midway between the upper and lower borders of the body of the mandible. In this and the previous specimen, there is no simian shelf.

No upper teeth have been found in direct association with the lower dentition of *L. legetet*. At Songhor in 1948, portions of two upper jaws with some of the maxillary teeth in position were discovered, which can be referred with some degree of probability to this species. One of these (S.120, 1948) contains the two premolars and the first molar excellently preserved and but little worn (Pl. 6, fig. 48), the basal half of the crown of the canine, and the roots of the two incisors (all of the right side). These teeth conform fairly accurately in their relative size, structure and occlusal relationships with the lower teeth in the mandibular fragment (C.M.H.104) of *L. legetet*. A small portion of the facial surface of the maxillary fragment is preserved, but shows no noteworthy features. The ridge overlying the root of the canine is bounded behind by a shallow canine fossa. The lower border of the base of the zygomatic process is seen rising just above the first molar. The upper canine has a well-marked internal cingulum which is prolonged back into a small notched "heel".

The antero-posterior diameter of the base of the crown is 5·4 mm., and the transverse 4·4 mm. The anterior premolar is of simple construction, the buccal and lingual cusps being nearly equal in size, and joined by a transverse ridge which merges with the anterior cingulum. Definite internal and posterior cingula are present. The posterior premolar is very similar in size and morphology to the anterior, except that the cingula are rather more strongly developed. The first upper molar shows a well-defined trigon with cusps of approximately equal size which are joined by even crests. The hypocone is clearly demarcated; it is continuous at its medial border with the internal cingulum, and is also joined to the base of the metacone by a low and inconspicuous enamel ridge. The internal cingulum forms a narrow rim with no secondary elaborations. The roots of the incisors are too broken to provide satisfactory measurements, but there is a diastema of approximately 2 mm. between the lateral incisor and the canine. The crown of an isolated second upper molar of the left side (S.101, 1948) was found in the same area and at the same time; it is almost identical in appearance with M $\underline{1}$ of specimen S.120, but is a little larger, and both may well belong to the same individual. The tooth is but little worn. The crown is of simple construction, with almost no secondary folding of the enamel. The three cusps of the trigon are well defined, and of approximately equal size. The hypocone is somewhat smaller; it is sharply demarcated from the cusps of the trigon, but is closely connected with the internal cingulum. The latter is distinct, but not complicated by secondary wrinkles. There is a faint external cingulum. A reconstruction of the upper dentition of *L. legetet,* based mainly on specimen S.120 and the isolated second upper molar is shown in text-fig. 27.

The other maxillary fragment from Songhor (S.59, 1948) comprises a small portion of the left side with the crown of the anterior premolar, and the roots of the incisors and canine. The premolar is similar in its crown pattern to that of the previous specimen, but is slightly larger. The facial part of the premaxillary suture is patent in the lower part of its course, and extends vertically upwards from the anterior margin of the canine. The width of the palate between the inner margins of the canine sockets is estimated to have been about 12 mm. The diameters of the roots of the incisors and canine at the alveolar border are as follows:

	a.p.	*tr.*
I $\underline{1}$	3·3 mm.	4·0 mm.
I $\underline{2}$	2·2 ,,	2·8 ,,
C $\underline{\ }$	5·4 ,,	4·2 ,,

The dimensions of the upper premolar and molar teeth in these two specimens are given in Table 9.

Incisors and Canines

In two specimens only (S.105, 1947, and 847 (R.1)), has an incisor tooth been found in direct association with a molar of *L. legetet.* In the first specimen, the tooth is a right lower incisor which shows considerable wear and was found adherent by matrix to a lower molar. Its total length is 15 mm. The height of the crown is almost 5 mm., and its maximum width 3 mm. The crown shows no outstanding features.

It resembles in shape and dimensions the corresponding tooth in *Hylobates*, except that the crown is relatively higher.

The other specimen (847), an isolated left upper central incisor, is almost certainly attributable to *L. legetet*. It has the spatulate form characteristic of a small hominoid, and was found in association with a lower molar belonging to this species. The dimensions of the crown are as follows: height 5·2 mm., width (estimated) 4·0 mm., antero-posterior diameter of base 3·7 mm.

Other isolated incisors provisionally assigned to *L. legetet* are: S.5, left I $\overline{1}$; S.44, left I $\overline{2}$; S.89, left I $\overline{2}$.

No complete canine teeth have been found directly associated with jaws or teeth of *L. legetet*. A number of isolated canines conform in their dimensions with those of the roots in the mandibular specimen S.120 and the maxillary fragment S.59. Three of these isolated canines are shown in Pl. 6, figs. 51, 52: S.3, 1947 (right upper canine) with the following crown dimensions: height 10 mm., antero-posterior diameter of base 6·0 mm., transverse diameter of base 4·0 mm.; C.M.H.20 (left lower canine from Songhor) with the following crown dimensions: height 7·6 mm., antero-posterior diameter of base 5·2 mm., transverse diameter of base 4·6 mm.; and S.17, 1947 (left lower canine) with the following crown dimensions: height 7.0 mm., antero-posterior diameter of base 5·2 mm., transverse diameter of base 4·0 mm.

Other isolated canines which are here attributed to *L. legetet* are as follows:

663, 1947 (R.1A)	Left lower canine.
C.M.H.44 (R.1)	Right upper canine.
602 R.106A	Right lower canine.
S.61, 1948	Right lower canine.
S.419, 1948	Right lower deciduous canine.
S.418, 1948	Left upper deciduous canine.

It is possible that some of these isolated teeth may be attributable to *Mesopithecus*, but, because of the paucity of remains of that catarrhine genus, such an interpretation seems improbable. Moreover, no other canine teeth of appropriate size have been recovered from the Miocene beds in Kenya which could reasonably be assigned to *L. legetet*.

Compared with *H. mulleri* (in which the molar teeth are comparable in absolute dimensions with those of *L. legetet*) the lower canines are shorter and have a less pronounced heel, while the upper canines appear to have been considerably shorter, and also much less recurved and less tusk-like in form.

Isolated Molars

The following molars have been referred to *L. legetet*, but their identification is not in all cases certain.

S.62, 1948	Left M $\overline{2}$ (slightly worn).
S.100, 1948	Left M $\overline{1}$ (damaged and considerably worn).
S.63, 1948	Left M $\overline{1}$ (very slightly worn) (Pl. 6, fig. 49).
S.64, 1948	Right M $\overline{1}$ (damaged and very worn).
S.1, 1948	Left M $\overline{3}$ (damaged and very worn).

S.105, 1947 . . .	Right M $\overline{2}$ (considerably worn; this tooth is adherent by matrix to a right lower incisor which presumably belonged to the same individual).
847, 1947 (R.1) . .	Left M $\overline{2}$ (slightly weathered; found in association with a left upper incisor).
S.416, 1948 . . .	? Left M $\overline{2}$.
39, 1947 (*Maboko*) . .	? Left M $\overline{2}$.
C.M.H.139 . . .	Left M $\overline{3}$ (weathered).
C.M.H.140 (R.1) . .	Right M $\overline{1}$ (much worn).

TABLE 9

LIMNOPITHECUS LEGETET

Upper Dentition

	P $\underline{3}$			P $\underline{4}$			M $\underline{1}$			M $\underline{2}$		
	a.p.	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*
S.120 . .	2·8	5·2	186	3·4	5·0	147	5·0	5·9	118			
S.59 . .	3·9	5·4	138									
S.101 . .										5·0	6·8	128

TABLE 10

LIMNOPITHECUS LEGETET

Lower Dentition

	P $\overline{3}$			P $\overline{4}$			M $\overline{1}$			M $\overline{2}$			M $\overline{3}$		
	a.p.	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*
L. legetet (holotype) . .							5·3	4·9	93	6·2	6·0	97			
S.13				5·0	4·6	92	5·6	4·8	86	5·7	5·6	98	6·5	5·2	80
C.M.H.104				4·8	3·5	73	5·6	4·5	80	6·0	5·1	85			
C.M.H.105	5·4	3·7	69	4·7	3·5	74	5·3	4·2	79	6·2	5·0	81	6·5	5·0	77
C.M.H.106							5·5	4·8	87	6·8	5·7	84			
C.M.H.108										6·2	5·3	85	6·2	4·8	77
S. 21, 1948 . . .										6·6	5·5	83	7·1	5·4	76
K.121, 1948 . . .													6·5	5·4	83
K.2, 1948										6·6	5·3	80			
S.5							5·5	4·3	78						
S.63							5·8	4·6	79						
Propliopithecus haeckeli Schlosser . . .	4·0	4·0	100	4·0	4·2	105	5·2	5·0	96	5·5	5·0	91	5·3	4·5	85

Limnopithecus macinnesi Le Gros Clark & Leakey

(see p. 13 for diagnosis)

In 1947, the two halves of the mandible of a new type of *Limnopithecus* were found at Wakondu on Rusinga Island (710, 1947). In the general features of the cusp pattern of the molar teeth, the specimen resembles *L. legetet* and without doubt (at least so far as dental morphology is concerned) represents a closely related hylobatine type (Pl. 7, figs. 53–55). However, it is considerably larger than *L. legetet,* and differs significantly in certain details of the dentition. We regard these differences as adequate for a specific distinction, and we have named the new species *L. macinnesi,* in recognition of the outstanding work which Dr. D. G. MacInnes has already completed on the Miocene primates from Kenya.

The mandible has suffered some distortion from crushing, so that only approximate measurements can be made on it. The two premolar teeth, and the second and third molars, are excellently preserved on both sides and show only a moderate degree of wear. The roots of the first molars are preserved, and also the root of the left canine. The incisor region of the left side is present, but the incisor sockets are only poorly defined. The dimensions of the mandible given below must be regarded as approximate estimates, for some correction for distortion has been attempted.

Height of body at level of P $\overline{3}$	20 mm.
Height of body at level of M $\overline{3}$	19 ,,
Thickness of body at level of M $\overline{2}$	8 ,,
Length of symphysis	22 ,,
Length of premolar-molar series	35 ,,

The mandible is lightly constructed, the height of the body being relatively low in comparison with its length. Herein the mandible contrasts rather strongly with that of *L. legetet* (including the specimens which were previously assigned to *L. evansi*), and more closely resembles *Pliopithecus* and *Hylobates.* There is a single mental foramen situated at the level of the interval between P $\overline{3}$ and P $\overline{4}$, and well below the centre of the body of the mandible. The anterior margin of the ascending ramus only slightly overlaps the posterior part of M $\overline{3}$.

The root of the left canine measures approximately 8 mm. by 5·5 mm. a little below the level of the alveolar margin. It appears not to be separated from the anterior premolar by a diastema, but there may have been a small gap which has been obliterated by crushing. P $\overline{3}$ is a distinctly specialized and almost caniniform tooth, being unicuspid, strongly compressed laterally, and acutely pointed. From the tip a sharp crest passes obliquely downwards in front; at its junction with the anterior end of the internal cingulum it produces a notch which is quite conspicuous from a lateral view. From this notch, the enamel extends considerably further down, forming an oblique anterior margin over the front of the anterior root. Less conspicuous ridges extend down from the tip of the cusp along the posterior and medial aspects of the latter to reach the cingulum. The internal cingulum is strongly developed and is directed obliquely backwards and downwards to form a small heel postero-medially. The crown of the anterior premolar is disposed very obliquely to the axis of the tooth (Pl. 9, fig. 55). The lateral surface of the crown is marked by a narrow elongated facet made by contact with the upper canine (which must therefore have overlapped the premolar to a marked extent, as in the modern gibbon). P $\overline{4}$ also shows some degree of specialization in its lateral compression and strongly pointed buccal cusp. It is bicuspid, but the lingual cusp is not so prominent as the buccal. The two cusps are united at their base by a low transverse crest which separates a small anterior fovea in front from an excavated talonid behind. The lateral surface of the main (buccal) cusp in its anterior part is strongly faceted by contact with the anterior upper premolar, and the downward extension of the facet clearly indicates a relatively long and projecting buccal cusp in that tooth. A strongly marked facet over the lateral aspect of the talonid of P $\overline{4}$ suggests that the buccal cusp in the corresponding upper premolar (P $\underline{4}$) must also have been well developed.

The first molar is missing on both sides; however, its antero-posterior diameter can be accurately estimated, for pressure facets show that it was in close contact with the neighbouring teeth. The antero-posterior diameter was 7·2 mm. (average of the two sides). Thus, as will be noted by reference to Table 12, the length ratio of M $\overline{1}$ to M $\overline{2}$ in *L. macinnesi* was 91—considerably higher than in any of the species of *Proconsul*. M $\overline{2}$ is approximately rectangular in its occlusal contour, the width of the trigonid and talonid being equal. The protoconid and metaconid are placed immediately opposite each other and are joined by a clear-cut and rather conspicuous transverse crest, the crista transversa anterior (or *hintere Trigonidleiste* of Remane's terminology). The latter marks the posterior boundary of a relatively large anterior fovea. The entoconid is likewise joined to the hypoconulid by a prominent crest which limits anteriorly a well-marked posterior fovea. The hypoconid is placed almost opposite the entoconid. Low ridges link the bases of the metaconid and entoconid medially and the protoconid and hypoconid laterally, so that the central talonid basin tends to be rather sharply circumscribed by these interconnecting crests. The hypoconulid is relatively smaller than in the corresponding tooth of *L. legetet;* it is displaced laterally to the median axis of the crown and comes rather closely in alignment with the protoconid and hypoconid. Except for faint traces antero-externally and postero-externally, there is no external cingulum. The last molar tooth is not markedly elongated; its breadth index is only slightly lower than that of M $\overline{2}$, and the cusp pattern is essentially the same. The anterior fovea is well marked and bounded behind by a strong crista transversa. There is a somewhat stronger indication of an external cingulum than in M $\overline{2}$, but this formation is not nearly as conspicuous as it is in *L. legetet*. The posterior fovea is distinct, and is bounded in front by a crest joining the hypoconulid to the entoconid. In both M $\overline{2}$ and M $\overline{3}$, the dentine has been exposed at the tips of the protoconid, hypoconid, and hypoconulid, while the tips of the metaconid and entoconid remain still almost unworn.

In their size and cusp pattern, the lower molars of *L. macinnesi* obviously resemble *Pliopithecus antiquus*. They differ, however, in their slightly higher breadth index (Table 12), the weaker development of the external cingulum, and the presence of well-defined crests uniting the cusps along the margins of the talonid basin. Also, the two premolars (especially P $\overline{3}$) show a higher degree of specialization. In all these features, the molars approach more closely to those of *Hylobates*, and *L. macinnesi* appears to be somewhat more specialized than the modern genus in that P $\overline{3}$ is more sectorial.

The symphysial region of a mandible (S.29) found at Songhor in 1947 can also be confidently referred to *L. macinnesi*, for it was associated with an isolated lower molar which conforms closely in its general dimensions and cusp pattern with the molars in specimen 710, 1947. The tooth is of hylobatine type, and too large to be ascribed to *L. legetet*. It is judged to be a first molar because of its relative breadth, the size and median position of the hypoconulid, and the relative positions of the protoconid and metaconid. Its length corresponds well with the estimated length of M $\overline{1}$ in specimen 710 (Table 12). The tooth is moderately worn, the protoconid is slightly in advance of the metaconid, but the hypoconid is almost level with the entoconid. The entoconid is somewhat reduced, and there is a trace of the external cingulum. The crown is slightly broader behind (6·5 mm.) than in front (6·0 mm.).

The symphysial fragment associated with this molar is illustrated in Pl. 7, fig. 56. It contains the right canine intact, the roots of three of the incisors, and the anterior root of P $\overline{3}$ of the right side. With it were also found the isolated left canine, the crown of an isolated left P $\overline{3}$, and an isolated left central upper incisor of a much smaller primate (possibly *L. legetet*). The roots of the central incisors at the level of the alveolar margin measure 4·0 mm. by 3·0 mm., and the corresponding measurements of the lateral incisor are 5·3 mm. and 3·2 mm. There is no diastema between the canine and the anterior premolar. The canine measures 26·5 mm. in total length, and the height of the crown is about 10 mm. The antero-posterior diameter of the crown at its base is 7·5 mm., and the transverse 5 mm. The tooth has been exposed to moderate wear, the posterior surface showing a flat facet for contact with an upper canine which was evidently a long and powerful tooth. There is a well-marked, shelf-like, internal cingulum which extends obliquely downwards and backwards to end in an excavated heel. The lower margin of the symphysis is not preserved in this specimen. The identification of the left P $\overline{3}$ found with the mandibular fragment is doubtful. While it conforms in size with the incisors and canines, it does not show the laterally compressed sharp-edged character seen in the corresponding premolar in the mandible 710, 1947. The type of wear is also different, the attrition facet made by the upper canine being situated on the anterior rather than the lateral aspect of the crown. Either the tooth is referable to some other small hominoid, or it indicates an unusually wide variability in the form of P $\overline{3}$ in *L. macinnesi*.

*C.M.H.*128 (*Rs*.17).—The anterior part of the left half of the body of a mandible containing the two premolars and the first molar in a much damaged condition. In their size, and the relative development of the talonid, the premolars conform closely with those of specimen 710, 1947, and the mandible appears to have been of the same light build (the vertical height of the body at the level of M $\overline{1}$ is 15·4 mm., and its maximum thickness at the same level 7·2 mm.). The first molar resembles that of *L. legetet* in its cusp pattern, but is much larger. The protoconid is slightly in advance of the metaconid, and the two cusps are joined by a rather well-defined crista transversa which forms the posterior boundary of a relatively deep anterior fovea. The hypoconid is placed nearly opposite the entoconid. The hypoconulid is small and almost median in position and is joined to the entoconid by a sharp crest. The talonid basin forms a relatively broad cup-shaped hollow. There is a distinct external cingulum posteriorly. This specimen was provisionally referred by MacInnes (1943) to the genus *Xenopithecus*, mainly on the basis of its general proportions. The additional material, however, indicates that it belongs to *L. macinnesi*.

S.9, 38 (MacInnes, 1943, pl. 23, figs. 9, 9a).—A small fragment of the left side of the mandible containing the two premolar teeth. $P\,\overline{4}$ is similar in its proportions and detailed characters to that of specimen 710, 1947, but it has a relatively larger talonid, and is a little larger in absolute dimensions (Pl. 7, fig. 57). The anterior premolar is a sectorial type of tooth in which the crown is almost entirely formed of the much hypertrophied buccal cusp. The whole tooth is strongly compressed laterally, and the enamel extends down some way on to the anterior aspect of the lateral root. The lingual cusp is no more than a minute tubercle on the crest which extends down from the tip of the main cusp to the internal cingulum. The latter is strongly developed, especially in front where it forms a distinct ledge. The tooth has a small talonid. The crown is obliquely disposed in relation to the axis of the tooth row. The anterior root of the first premolar is exposed in this specimen—it has a length of 14·5 mm.

Associated(?) Upper and Lower Teeth of *L. macinnesi*

Upper and lower teeth of *L. macinnesi* have not so far been discovered in direct association,* but fragments of maxilla and mandible found on Rusinga Island (593, 1947, R.106A, and C.M.H.126, Rs.103) may have belonged to the same individual. The maxillary fragment was found in 1947, at a site quite close to the position where the mandibular fragment had been picked up on the surface at an earlier date. They are both immature specimens, showing an equivalent stage of dental eruption, and a similar degree of weathering. The maxillary fragment (593, 1947) is of the left side and contains $M\,\underline{1}$ and $M\,\underline{2}$, the latter probably quite recently erupted. The dimensions and cusp patterns of these teeth correspond closely with those of the more complete upper dentition of specimen 545 (described below), also from site Rs.106A. In front of $M\,\underline{1}$, the unerupted crown of $P\,\underline{4}$ lies embedded in the alveolus, and has been partly exposed. In its dimensions, in the relative size and shape of the cusps, and in the development of the anterior and internal cingulum, it agrees quite closely with the corresponding tooth in specimen 545 (see below). A right upper canine was found with the maxillary fragment; it is considerably weathered and has lost the tip. In its dimensions and shape, including the appearance of the vertical groove on its anterior aspect, the tooth agrees closely with the canine in the maxillary fragment (S.57) (see below). The mandibular fragment (C.M.H.126), from the right side, contains a small broken fragment of $M\,\overline{1}$, the recently erupted (and unworn) $M\,\overline{2}$, and the unerupted crown of $M\,\overline{3}$ still embedded in the alveolus. The second and third molars correspond very closely indeed in dimensions and cusp pattern with those of specimen 710, 1947. The posterior fovea is relatively large in both teeth, and is bounded anteriorly by a crest (particularly distinct in $M\,\overline{3}$) uniting the entoconid to the hypoconulid. The external cingulum is only weakly developed.

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* Since writing this, the upper and lower dentitions of *L. macinnesi* have been found in direct association. This discovery confirms the identifications of the upper teeth which have been made in this monograph.

Apart from the specimens described above (whose association is probable but not certain), none of the specimens of the lower dentition of *L. macinnesi* described in this monograph has been found in direct association with maxillary teeth. However, some maxillary fragments and isolated upper teeth from Rusinga and Songhor are certainly attributable to this species. They conform in size, proportions, and cusp pattern with the upper molar teeth of specimen 593, 1947, and are considerably larger than those ascribed to *L. legetet*. In certain features, also, the canine and premolars appear to harmonize well with the corresponding mandibular teeth in specimen 710, 1947.

The most complete of these specimens is a palate and upper dentition (Pl. 7, fig. 58) found at the site R.106A on Rusinga Island in 1947 (No. 545). It has been exposed to weathering and is in two halves, but part of the mid-line is preserved on the left side. All the premolars and molars are present on each side, and are only slightly worn, but they show varying degrees of weathering. The outer part of the left first molar has been broken off. The bases of the canines are also preserved, more completely on the left side than on the right. The roots of the two left incisors and of the right lateral incisor are present. Only that part of the facial aspect of the maxilla which is immediately adjacent to the alveolar border is preserved, and (on the left side) a very small extent of the lower border of the nasal aperture. The lower border of the base of the zygomatic process is situated close to the alveolar border, immediately above the second molar tooth. The width of the palate can only be approximately estimated, since it is not possible to define the mid-line accurately, though there is some indication of it in the left fragment. For the same reason, the degree of divergence of the tooth rows is slightly conjectural, but reference to the incisor sockets and the preserved mid-line of the palate indicates that the divergence was not marked. The width of the palate between the inner margins of the canines is estimated to be about 12 mm., and between the inner margins of the first molars about 14 mm. The total length of the premolar-molar series is 27 mm.

The canine is a relatively stout tooth; the base of the crown measures 6·6 mm. by 5·5 mm. From the preserved portion of the crown on the left side its total length from the alveolar border is estimated to have been about 12 mm. There is a well-marked internal cingulum, and the anterior surface of the crown is marked by a deep vertical furrow. Between the lateral incisor and the canine is a small diastema measuring a little over one millimetre. The anterior premolar shows some degree of specialization in the relatively great length of the buccal cusp, the pointed extremity of which projects well beyond the level of the posterior premolar. The cusp is laterally compressed and bounded in front and behind by sharp borders. The total height of the buccal cusp from the base of the enamel is 7·0 mm., whereas that of the lingual cusp is 3·8 mm. This sub-caniniform character of $P\,\overline{3}$ would account well for the elongated attrition facet already noted on the lateral surface of the crown of $P\,\overline{4}$ in specimen 710, 1947. The anterior and posterior cingula of $P\,\overline{3}$ are quite distinct. In the posterior premolar the two cusps are not sharply contrasted in size, though the buccal cusp is the larger. The height of this cusp from the base of the enamel is 4·7 mm. The internal cingulum in $P\,\underline{4}$ is conspicuous.

The simple cusp pattern of the upper molars is unelaborated by secondary enamel foldings (Pl. 7, fig. 58). In M $\underline{1}$ the three cusps of the trigon are of almost equal size, the protocone being slightly larger than the others, and they show some degree of convergence which constricts the relative size of the trigon. They are interconnected by low ridges along the margins of the trigon, and a low crest also extends from the front of the protocone down to the anterior cingulum. The hypocone is distinctly circumscribed, but it is considerably smaller than the cusps of the trigon. It is directly continuous with the internal cingulum and is not sharply demarcated from the latter. Laterally it is separated from the metacone by a broad sulcus, but the bases of the two cusps are linked across the bottom of this sulcus by a low ridge of enamel. Behind this ridge is a small localized depression—the posterior fovea. The internal cingulum is present as a simple rounded rim, which is continuous with the anterior cingulum in front and extends without interruption to the apex of the hypocone behind. In M $\underline{2}$ the cusp pattern is essentially the same, except that the internal cingulum is more strongly developed, and is faintly crinkled; the hypocone is relatively smaller—appearing as little more than a local eminence of the internal cingulum interrupting the continuity of the latter with the posterior cingulum. The enamel ridge connecting the base of the hypocone with the metacone is rather better marked than in M $\underline{1}$. M $\underline{3}$ shows signs of reduction. The metacone is much diminished in size, and the hypocone even more so. The internal cingulum is relatively broad and somewhat complicated by wrinkling. The occlusal surface of the crown of M $\underline{3}$ is narrowed posteriorly, and thus has a sub-triangular contour. On the lateral aspect of each of the upper molars there is a very faint trace of an external cingulum.

S.57 (Pl. 7, figs. 59, 60).—This specimen, found at Songhor in 1948, consists of an excellently preserved fragment of the left side of the upper jaw, including the premaxillary region with the medial and lateral incisors intact, the adjacent part of the margin of the nasal aperture, the front part of the palate with the incisive foramen, the canine (the tip of which is missing), and the two premolars. The total width of the entire palate between the inner margins of the canines can be reliably estimated to have been 20 mm. The distance between the lower margin of the nasal aperture and the alveolar margin in the mid-line is 9 mm. As may be seen by reference to Pl. 7, fig. 59, the sub-nasal surface of the premaxilla slopes downwards and forwards so that the incisors are set at an oblique angle. A conspicuous diastema, 3·5 mm. in width, separates the lateral incisor from the canine. Traces of the premaxillary suture can be seen in the palate and the lower part of the facial surface, but its course cannot be traced with confidence.

The central incisor has the characteristic spatulate form. Posteriorly, it shows a cingular ridge thickened centrally to form a small basal tubercle. The maximum width of the crown is 6·4 mm., its height 6·5 mm., and its antero-posterior thickness at the base 4·5 mm. The lateral incisor is much smaller, the height of the crown being 5·6 mm. and its maximum width 3·2 mm. The biting edge is disposed obliquely, and the lateral margin of the crown is notched by an attrition facet made by contact with the lower canine. The upper canine is a relatively large tooth, rather strongly recurved, and elongated into a tusk-like form. Its anterior rounded border is scored by a deep vertical groove, while the posterior border has been converted into a sharp edge by attrition with P $\overline{3}$. The enamel on the outer and inner surfaces is faintly ribbed by longitudinal ridges. The internal cingulum is not strongly developed. The diameters of the base of the crown are 8 mm. by 6·5 mm., and the total length of the crown from the alveolar margin to the tip is estimated to have been about 15 mm. The long and sabre-like upper canine indicates a sectorial lower front premolar such as we have already noted in the mandible of specimen 710, 1947. It has already been pointed out, also, that the elongated attrition facet on the lateral surface of P $\overline{3}$ in specimen 710 would have required for its production a canine of this type.

The premolars are slightly narrower than in specimen 545, 1947, but otherwise show much the same characters. They have been exposed to more wear and from this point of view are not so readily comparable. The buccal cusp in P $\underline{3}$ is considerably the longer of the two cusps. Its height from the basal margin of the enamel is 5·4 mm., whereas that of the lingual cusp is only 2·5 mm. The internal cingulum is lacking in P $\underline{3}$, but it is well developed in P $\underline{4}$ (as in the previous specimen). The two cusps in the latter are sub-equal in size.

908, 1947 (*R. Kiahera Hill*).—A small fragment of the left maxilla, with the three molars in position. The teeth have been considerably weathered and are also partly worn. They correspond closely in the details of their cusp pattern with the molars in specimen 545, 1947, but are somewhat smaller in general dimensions. Some fragments of skull cap were found in association with the maxillary fragment, but they are indeterminate.

*C.M.H.*107 (*Songhor*).—Fragment of right side of the mandible with the first molar excellently preserved and almost unworn. Behind it is the stump of the second molar, and behind this again a portion of the socket for the third molar, which was probably unerupted. In the first molar there is a distinct external cingulum which is continued round to the back of the crown as a rather definite posterior cingulum. In this character it resembles the lower molars of *L. legetet*, but, apart from the size of the tooth, the distinctness of the crista transversa and anterior fovea gives it a close resemblance to the M $\overline{1}$ of *L. macinnesi*. The protoconid is well in advance of the metaconid so that the front half of the crown has a distinctly "skew" appearance. The height of the body of the mandible at the level of M $\overline{1}$ is 18 mm.

*C.M.H.*127 (*R.*91).—Fragment of right side of lower jaw containing in a much worn and weathered condition the second and third molars, and the roots of the first molar. In their size the teeth conform closely with the corresponding teeth of specimen 710, 1947, but, so far as can be estimated in their damaged state, M $\overline{3}$ is somewhat narrower.

Isolated teeth.—A collection of associated hominoid upper teeth (1011–1022) found near Survey Beacon No. 2 on Rusinga Island (R.113) can with certainty be ascribed to *L. macinnesi*. They are severely worn, but retain sufficient details to show that the cusp pattern was probably identical with that of the upper molars of specimen 545, 1947. The following teeth in this series are present: right I $\underline{2}$, left C, left P $\underline{4}$, the badly weathered remains of the two right premolars, all the molars (of which the right M $\underline{3}$ is broken). The lateral incisor is similar in general dimensions to that of specimen S.57 except that the biting edge (4·4 mm.) is somewhat broader.

The canine corresponds closely in its form and size with that of S.57. The anterior aspect is scored by a pronounced vertical furrow, and posteriorly it is deeply worn by attrition with the anterior lower premolar. The tip of the crown and the tip of the root have been broken off. The total length of the tooth is estimated to have been about 31 mm. The left posterior premolar is narrower than the corresponding tooth in S.57 and the internal cingulum is conspicuous. The dimensions of this tooth and the molars are shown in Table 12.

S.411, 1948.—This specimen consists of an isolated right central upper incisor, perfectly preserved. In shape and dimensions it is almost an exact counterpart of the central incisor in the maxillary specimen S.57. The biting edge measures 5·5 mm. transversely and the maximum height of the crown is 7·6 mm.

S.H. (Pl. 7, fig. 62).—Left upper central incisor, much worn, with dimensions closely approximating to those in specimen S.57.

*C.M.H.*40–43.—Four isolated upper canines which, in their dimensions and morphology, closely resemble the upper canines in the maxilla (S.57), and are thus almost certainly referable to *L. macinnesi*. The locality of C.M.H.40 is not known; the other three teeth were found on Rusinga Island (R.1, R.38, and R.91).

S.7 (Pl. 7, fig. 63) *and S*.88, 1948.—Two isolated left lower canines which, on the basis of size and resemblance to the lower canines in specimen S.29, are provisionally referred to *L. macinnesi*.

The following specimens of isolated molars collected in the Kavirondo area have been identified as those of *L. macinnesi*.

Upper molars

667 (*R*.)	Crown of right M $\underline{1}$ (probably unerupted). In dimensions this tooth corresponds closely with the first molar of specimen 545. In detail, the external cingulum is more pronounced, and the internal cingulum shows distinct beading. A low ridge connects the hypocone with the metacone, and also with the protocone (Pl. 7, fig. 61).
546 (*R*.106*A*)	Right M $\underline{2}$ (slightly worn).
814 (*R*.1)	? Left M $\underline{1}$ (unerupted). There is some doubt about the identification of this tooth—it may be a deciduous molar of a larger species.
S.415, 1948	Right M $\underline{2}$ (unworn).
S.417, 1948	Right M $\underline{3}$.
S.407, 1948	Left M $\underline{3}$ (much worn).
C.8 (*Rs*.)	Right M$\underline{2}$ (moderately worn). There is some doubt about the identification of this tooth—it differs from other specimens in the absence of an internal cingulum (except anteriorly at the base of the protocone), and the hypocone is rather more strongly developed. In its general size and proportions, however, as well as in the simplicity of the cusp pattern, it appears to be referable to *L. macinnesi*.

Lower molars

*C.M.H.*125 (*R.*1)	M $\bar{3}$ (moderately worn). This tooth differs from the last molars in specimen 710, 1947, in its lower breadth index, and in the fact that the hypoconulid is in alignment with the metaconid and hypoconid. The talonid basin is relatively broad and shallow, and there is a narrow external cingulum. The crista transversa anterior is distinct.
503 (*R.*1*A*)	Left M $\bar{1}$. The identification of this tooth as a first molar depends on its size and on the relatively forward position of the protoconid. In its cusp pattern it shows a close resemblance to the first lower molar of *L. legetet,* but it is larger, the hypoconid and entoconid are placed directly opposite each other, and the posterior fovea is well developed. Segments of a small external cingulum are present at the interval between the protoconid and hypoconid, and at the antero-external margin of the crown. The tooth differs from M $\bar{1}$ in specimen S.29 in having a lower breadth index.
*S.*99, 1948	Left M $\bar{1}$ (moderately worn). The external cingulum is only faintly indicated in the sulcus separating the protoconid from the hypoconid.
*S.*122	Right M $\bar{1}$ (severely worn).
*C.M.H.*138 (*R.*1)	Left M $\bar{3}$ (moderately worn).

The Relationship of *L. macinnesi* to *L. legetet.*—In its basic features the dentition of these two species is very similar. The question arises whether the differences which we have noted are adequate for establishing a specific distinction. The size relationships of the molar series as a whole are insufficient if a comparison with the modern gibbon is justified. For example, according to Remane's data (1921) the percentage ratio of the greatest length of the lower molars to the smallest length in a single species (*Hylobates concolor*) may be almost 150 per cent.; the corresponding ratio in all the specimens of the genus *Limnopithecus* is 138 per cent. On the other hand, if the frequency distribution of the lengths of all the known specimens of lower molars in *Limnopithecus* is plotted, the graph in the case of each molar shows two well-marked peaks corresponding to the two species which have been defined. These results may simply express a sexual dimorphism, but the peaks appear to be too sharply separated to support this interpretation. Moreover, there is an interesting contrast in the localities where the remains of the two species have been found. Out of forty specimens of *L. legetet,* thirty-two are from Songhor and Koru, and only eight from Rusinga Island. On the other hand, out of thirty-four specimens of *L. macinnesi,* no less than twenty-one come from the Rusinga deposits. Differences in the details of the cusp pattern of the teeth, apart from their size, also seem to justify a specific distinction. These may be summarized as follows. The upper canines in *L. macinnesi* are relatively longer and more sabre-like in form, and the upper anterior premolar is characterized by the height of its buccal cusp which is strongly compressed laterally with sharp anterior and posterior borders. In the upper molars the internal cingulum is quite simple in *L. legetet,* whereas in *L. macinnesi* it shows a fine beading. The anterior lower premolar in *L. macinnesi* shows a marked specialization in its sharply compressed form and in the extension downwards of the enamel on to the anterior root. In the lower molars the cusps are more individualized in *L. legetet,* whereas in *L. macinnesi* they tend to be interconnected at the margins of the talonid basin. Thus, the crista transversa anterior, linking the protoconid and metaconid, is represented in the former species by a low and inconspicuous fold of enamel, whereas in the latter it forms a relatively sharp ridge; consequently the anterior fovea is more clear cut in *L. macinnesi.* Again, in the larger species, the hypoconulid is connected to the entoconid by a crest (*hintere Hauptleiste* of Remane's nomenclature) which may be very sharply defined, and this is accompanied by the development of a well-marked posterior fovea (particularly in the last molar). In *L. legetet* the posterior fovea is commonly small and shallow, or even absent altogether. The external cingulum is strongly developed in *L. legetet;* in *L. macinnesi* it is usually represented by weak remnants or may be entirely missing. Lastly, the hypoconulid is relatively rather smaller in *L. macinnesi,* and the hypoconid and entoconid are placed at almost the same level (whereas in *L. legetet* they tend to occupy an alternating position). Apart from dental characters, the relative length, and also the slenderness of construction, of the body of the mandible in *L. macinnesi* offers a point of contrast with *L. legetet* which certainly has some taxonomic significance.

Taking all these features into consideration we feel justified in making a specific distinction between *L. legetet* and *L. macinnesi.* In general, *L. macinnesi* is more specialized in its dental characters (approximating in a number of features more closely to the recent Hylobatinae); in size it appears to bear a relationship to *L. legetet* somewhat similar to that between the modern hylobatine genera *Symphalangus* and *Hylobates.*

TABLE II

LIMNOPITHECUS MACINNESI

Upper Dentition

	P $\underline{3}$			P $\underline{4}$			M $\underline{1}$			M $\underline{2}$			M $\underline{3}$		
	a.p.	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*
545	4·2	6·5	155	4·1	6·4	156	5·8	7·1	122	6·4	7·7	120	6·2	7·6	123
S.57	4·4	5·8	132	4·2	5·8	138									
667							5·7	6·8	119						
546										6·4	7·6	119			
1011–1022	3·9	6·6	169				6·7	7·8	116	7·3	8·6	118	6·0	7·6	127
593							6·1	—		6·9	—				
S.415										6·3	7·8	124			
S.47													5·3	6·7	126
908							5·5	6·8	124	5·8	6·7	116	5·2	6·4	123
Pliopithecus antiquus Gervais (Hofmann)	4·5	6·0	133	4·5	7·0	156	6·3	7·4	119	7·0	8·0	114	6·5	7·5	115

Table 12

LIMNOPITHECUS MACINNESI

Lower Dentition

	P $\overline{3}$			P $\overline{4}$			M $\overline{1}$			M $\overline{2}$			M $\overline{3}$			M $\overline{1}$/M $\overline{2}$	M $\overline{2}$/M $\overline{3}$
	a.p.	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*tr.*	*ind.*	*a.p.*	*a.p.*
710 . . .	7·7	4·6	60	6·1	4·7	77	7·2 est.			7·9	6·7	85	7·9	6·7	85	91	100
S.29 . . .							7·3	6·2	85								
C.M.H.125 . .										8·1	6·3	78					
503 . . .							7·2 est.	5·3	74								
C.M.H.126 . .										7·9	6·4	81					
C.M.H.107 . .							6·7	5·2	78								
C.M.H.127 . .										7·6	6·4	84	8·4 est.	6·4	76		90
S.99 . . .							7·2	5·8	81								
C.M.H.128 . .				5·0	4·2	84	7·0	6·0	86								
S.9, 1938 . .	8·1	4·6	57	6·0	5·3	88											
Pliopithecus antiquus Gervais (Hofmann) . .	6·0	4·5	75	5·0	5·0	100	6·2	5·5	89	7·3	6·0	82	7·5	6·0	80	85	97

Table 13

TOTAL LENGTH OF PREMOLAR-MOLAR SERIES IN *LIMNOPITHECUS* AND *PROCONSUL*

		Upper	*Lower*
Limnopithecus legetet . . .	S.120 and S.101	23	—
	S.13	—	27
	C.M.H.105	—	28·5
L. macinnesi	545	27·5	35
Proconsul africanus . . .	M.14084	38	—
	R.1948, 50	36	43·5
	C.M.H.102	—	43
	R.1948, 375	—	41
P. nyanzae	C.M.H.2	48·5	—
	C.M.H.3 and 4	49·5	55
	M.14086	—	52
	S.28	—	53
	1942 mand. and 712	42	45·5
P. major	S.80, 1947	—	66

Limb Bones

A few isolated limb bones attributable to some of the large hominoids have come to light. Although they are from sites which have also yielded teeth and jaws of *Proconsul,* none of those to be described in this section was found in such close association with these other remains as to permit any assurance that it belonged to the same individuals. However, since limb-bone fragments of fossil anthropoid apes are everywhere so extremely rare, it seems desirable to give a general description of those found in Kenya even if their identification is uncertain. A full analysis of their morphological features would be premature, since further material which has not yet been developed and made available for study has already been discovered.

Tarsal bones.—A perfectly preserved right talus (C.M.H.145) of a large primate was found in the Miocene deposits at Songhor, in direct association with a right calcaneum (C.M.H.146). The two bones evidently belonged to the same individual. A left talus of similar size (C.M.H.147), and equally well preserved, was recovered from Kalim on Rusinga Island in 1941. These specimens have been described by MacInnes (1943) who pointed out that, though they are similar in several respects to the tarsal bones of a chimpanzee, they also show some significant differences. He ascribed them to the genus *Proconsul,* and there seems to be reasonable justification for this view. They were recovered from deposits which had also yielded teeth of *Proconsul,* and their size conforms with that of *Proconsul* so far as this can be estimated from the teeth and jaws. Their general proportions and appearance at once suggest the tarsal bones of a large primate, and the only remains of large primates of conformable size from the Miocene deposits in the same area are almost all attributable to the genus *Proconsul.* Of the different species of *Proconsul,* they are most likely to belong to *P. nyanzae,* partly because of their general dimensions and partly because the remains of this species are the most common. There is one other possibility—that these tarsal bones belong to the species which is here called *Sivapithecus africanus.* However, remains of this type are very rare, and none of them was found in close relationship to the tarsal bones.

Talus.—The fossils resemble the talus of a chimpanzee in size and general proportions (Pl. 8, fig. 64). They differ in the relatively small and more sharply curved articular head, the more slender and relatively longer neck, the pronounced cup-shaped hollow at the anterior end of the medial malleolar facet, and the extent and disposition of the sustentacular facet. The main dimensions in millimetres of the two bones are as follows:—

	Total length	*Max. width of articular head*	*Max. ht. of head*	*Length along median axis of superior facet*	*Width of ant. margin of superior facet*	*Width at middle of superior facet*	*Width of post. margin of sup. facet*	*Ht. of lat. malleolar facet*
C.M.H.145 .	52	21	18	27	24	20	14	22
C.M.H.147 .	45	21	18	24	20	17	13	21

In the relative size and shape of the articular head, the fossil tali approach the orang rather more closely than the chimpanzee and gorilla, for in the two latter genera the head is much broader and flatter. They differ from the orang and the other recent large apes, however, in the greater lateral extent of the articular surface, which presumably allowed for a greater degree of eversion of the fore part of the foot at the transverse tarsal joint, and also for a more even transmission of weight to the navicular and three cuneiform bones, than occurs in the modern Ponginae. In this respect, and also in the relative length of the neck, the fossil bones show a closer resemblance to the talus of the gibbon and of the cercopithecoid monkeys. In the details of the neck, they display certain other features characteristic of the cercopithecoids rather than of the anthropoid apes.

These features of the talar neck are related to the "locking" of the ankle-joint in full dorsi-flexion by the accurate apposition of the lower extremity of the tibia in this position. On the medial aspect of the neck is a cup-shaped hollow formed by the forward extension of the medial malleolar facet, and on the upper surface is a circumscribed faceted tubercle, on the front of which is a backward extension of the articular surface of the head of the bone. This tubercle may be termed the "dorsal tubercle of the neck" of the talus. A comparison with the limb skeleton of Old World monkeys shows that in dorsi-flexion the excavation at the anterior end of the malleolar facet accommodates the anterior margin of the medial malleolus, while the dorsal tubercle fits neatly into a notch on the anterior margin of the lower extremity of the tibia immediately lateral to the malleolus.

In the modern anthropoid apes these features are but feebly developed. In the chimpanzee there is a slight malleolar concavity, but not a pronounced cup-shaped hollow as in the fossil bones. A dorsal tubercle is also commonly present, but it is ill-defined, not faceted, and distinct from the articular surface of the head. In the gorilla, orang, and gibbon the malleolar hollow can hardly be said to be present, and the dorsal tubercle is ill-defined or absent. In some of the Cercopithecoidea, on the other hand, these features are as strongly developed as they are in the fossil bones. Particularly is this the case in *Papio*, *Macaca*, and some of the langurs. In specialized arboreal types such as *Ateles*, on the other hand, they are absent, or but feebly represented.

On the inferior surface of the neck in the fossil tali, the sustentacular facet extends backwards and laterally as an elongated tongue-shaped process. In the chimpanzee talus (Pl. 8, fig. 64c) this process is shorter (in relation to the shorter neck) and extends more obliquely backwards towards the medial aspect of the bone. This disposition, which is common to all the recent Pongidae, permits a considerable range of medial rotation of the sustentaculum of the calcaneum on the under surface of the talar neck and thus allows for the marked degree of inversion which characterizes the feet of the modern anthropoid apes. In the cercopithecoid foot, on the other hand, the sustentacular facet on the neck of the talus is commonly disposed as it is in the fossil bones.

The body of the talus in either fossil specimen is similar in its general proportions to that of the chimpanzee, but the main tibial articular surface is relatively somewhat narrower, and does not broaden out so conspicuously towards its anterior margin. In these characters of the articular surface, the resemblance is again with the cercopithecoid talus rather than with that of any of the recent Pongidae. One other feature merits attention—the roughened areas, eminences, and depressions for the attachment of ligaments are strongly pronounced in the fossil bones, more so, relatively, than is commonly found in the modern anthropoid apes.

Calcaneum (Pls. 8 and 9, figs. 65–68).—The calcaneum (C.M.H.146) found at Songhor in direct association with one of the tali is well preserved except for the heel process. MacInnes has recorded some of the main features of this specimen, and has particularly drawn attention to the strong development on the plantar surface of the basal tubercle. In its general size and proportions, the fossil calcaneum is comparable with that of a female chimpanzee. It differs from the chimpanzee in the smaller size of the sustentaculum, in the greater posterior extension of the main talar facet, and in the relatively greater length of that part of the bone which lies in front of the main talar facet.

The oval main talar facet is more elongated than is commonly the case in the chimpanzee and other modern anthropoid apes (measuring 24 mm. in the long axis and 17 mm. in the transverse). Moreover, unlike the modern apes, the greater part of its long axis lies *behind* the level of the posterior border of the sustentacular tali at its attachment to the body. This contrast is well shown in Pl. 9, fig. 67. Its lateral margin is interrupted by a small sharply cut notch which lies opposite a rough depression behind the lateral malleolar facet of the talus when articulated with the latter, and which evidently served for the attachment here of a strong talo-calcaneal ligament. A similar notch, though less pronounced, is sometimes present in the calcaneum of the chimpanzee. Immediately in front of the notch is a slight eversion of the main talar articular surface forming an oval facet presumably related to part of the lateral talo-calcaneal ligament.

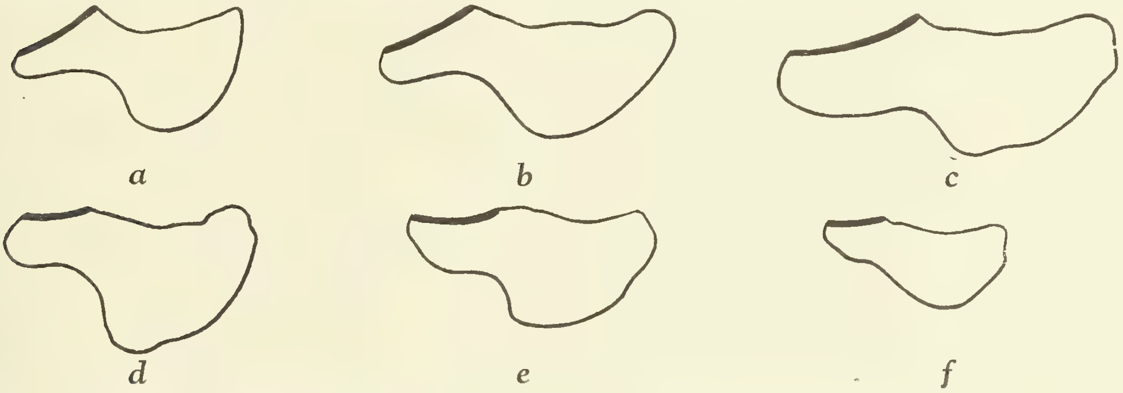

FIG. 21. Transverse sections through the calcaneum (at a level immediately in front of the main talar facet) of (a) orang, (b) chimpanzee, (c) gorilla, (d) ? *Proconsul*, (e) gibbon, (f) *Nasalis* monkey. The articular surface of the sustentaculum is indicated by a thickened line. The diagrams are all natural size with the exception of that of the gibbon, which is twice natural size.

The sustentaculum tali bears a relatively small oval and slightly concave facet. If the calcaneum is orientated so that the flat dorsal surface in front of the main talar facet is horizontal, the sustentacular facet is found to face almost directly upwards. Herein it contrasts with the modern large anthropoid apes in which, with a similar orientation of the calcaneum, the sustentacular facet shows a marked medial inclination (text-fig. 21). This medial inclination partly accounts for the degree of sub-talar inversion of the foot which is characteristic of the modern apes. It may also have some relation to the body weight of these animals, for in the small gibbon the facet does not slope medially to the same extent. In the cercopithecoid monkeys, the sustentacular facet is similar in its orientation to that of the fossil specimen. Anteriorly, the sustentacular facet is continuous, through a narrow constriction, with a facet for the head of the talus at the front end of the medial margin of the calcaneum, as is also not uncommonly the case in the chimpanzee.

The facet for articulation with the cuboid forms a deeply cupped crescentic excavation, open below where it leads into a rough pit for the attachment of the plantar calcaneo-cuboid ligament. The excavation of the articular surface is distinctly more pronounced that it is in the modern apes, though it is approached in this respect by the orang. While permitting some degree of rotation between the cuboid and calcaneum about an axis represented by the plantar calcaneo-cuboid ligament, it must severely limit any lateral displacement between the two bones and thus add considerably to the strength of the joint.

The sustentaculum is marked on its under surface by a broad groove for the flexor hallucis longus tendon; lateral to this, there is a remarkably well developed basal tubercle. The significance of this tubercle in the Primates has been discussed at some length by Weidenreich (1921), who points out that in the quadrupedal monkeys it forms a supporting eminence through which the weight of the body is transferred to the ground, and that even in the anthropoid apes it partly serves this function. In the fossil bone the basal tubercle is relatively more prominent and circumscribed than in the modern apes; it is also situated more posteriorly in relation to the sustentaculum. The summit of the tubercle lies vertically below the anterior margin of the main talar facet of the calcaneum. In this relatively posterior position the basal tubercle contrasts markedly with those of the modern apes and cercopithecoid monkeys and leads to the inference that in *Proconsul* the component of the animal's weight transferred to the ground through the body of the calcaneum may have been directed more backwards towards the heel. Unfortunately, the calcaneal tuberosity is missing in the fossil specimen, so that it is not known whether the plantar extension of the tuberosity was developed as it is in the modern anthropoid apes. However, according to Weidenreich (1946), even in the chimpanzee and gorilla, in which the plantar process is prominent, the heel itself scarcely touches the ground when the animal is standing or walking on a plane surface, the foot resting mainly on the front part of the calcaneum and the cuboid. The tentative inference from the disposition of the basal tubercle, that *Proconsul*, if it occasionally raised itself up into an erect position, may have been capable of balancing more securely on the calcaneal region of the foot than is possible in the modern apes, agrees well with the observation that in the fossil bone the greater part of the main talar facet (through which the body weight is transmitted to the calcaneum) lies behind the level of the posterior border of the sustentaculum, thus permitting a greater proportion of the body weight to be transferred through this articulation backwards to the calcaneal region. The lateral surface of the calcaneum shows an elongated peroneal process similar to that of the chimpanzee. In the fossil bone its surface has been eroded.

The general orientation of the calcaneum, in comparison with that of the chimpanzee, can be readily apprehended by reference to text-fig. 22, in which the anterior aspect of the talus and calcaneum (articulated together) is shown. In both the fossil specimen and the chimpanzee, the calcaneum has been inverted to the extreme limit of its articular surfaces on the under surface of the talus, and the bones are orientated so that the summit of the upper surface of the main tibial facet of the talus is horizontal. In the chimpanzee, as in other modern representatives of the Ponginae, the inversion of the calcaneum, as shown by the medial position of the concave depression in the margin of the facet for the cuboid, is much more pronounced, and the lateral surface of the calcaneum faces directly downwards. Evidently, therefore, the foot of *Proconsul*, even in the fully inverted position, did not rest so completely on the outer margin of the foot. Manipulation of the talus and calcaneum in articulation with each other demonstrates that it was also capable of a greater degree of eversion at the sub-talar joint.

Functional implications of the talus and calcaneum.—In the absence of a more complete skeleton of the foot, conclusions regarding the functional implications of the talus and calcaneum ascribed to *Proconsul* are necessarily tentative. Nevertheless, they provide indications regarding the mechanism of the foot which are of considerable interest. The relative length of the talar neck and the front part of the calcaneum shows that in this fossil hominoid the anterior tarsal segment had not undergone the shortening which is characteristic of the modern large apes. Morton (1924) has drawn attention to the significance of this shortening and has inferred from his comparative studies that it is related to an extreme form of arboreal specialization, and that it could hardly have been present in the early ancestors of the Hominidae. The proportions of the fossil bones must have been correlated with a relative length of the anterior tarsal segment of the foot comparable with that of the quadrupedal cercopithecoids, providing an effective leverage from the heads of the metatarsal bones in movements of leaping and running. The orientation of the calcaneum in respect of the talus, the plane of the sustentaculum, and the disposition of the articulation between the latter and the head of the talus, together show that the foot was held in a more everted plantigrade position similar to that of the cercopithecoid foot, and strongly suggests quadrupedal functions whether on the ground or among the branches of trees. The size of the large Miocene hominoids, however, would no

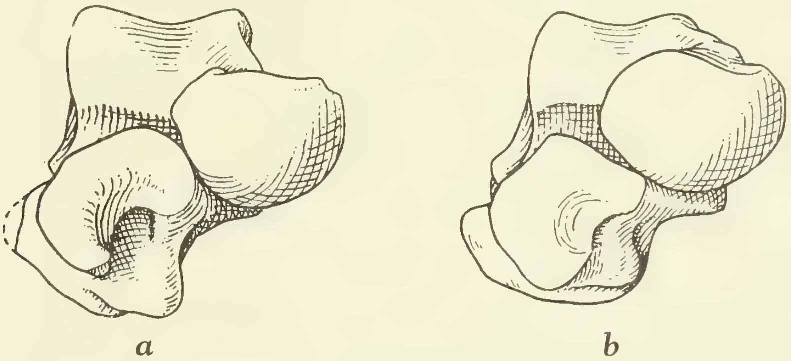

Fig. 22. A. The talus and calcaneum (C.M.H.145 and 146) of ? *Proconsul* viewed from in front and compared with B. Those of a male chimpanzee. Natural size. In both cases the calcaneum has been inverted to the extreme limit of its articular surfaces on the under surface of the talus.

doubt have precluded much activity of this sort in the trees. That the foot skeleton was designed for bearing strains and stresses associated with rapid running movements, rather than for the greater mobility required for specialized arboreal habits, is further indicated by the strong impressions for the ligamentous attachments to the talus and calcaneum, as mentioned above, as well as by the deep excavation of the facet on the calcaneum for the cuboid bone. Evidently the tarsal elements formed a stronger and more firmly knit mechanism than in the modern large apes. The cup-shaped hollow at the anterior end of the medial malleolar facet on the talus, and the strong development of the dorsal tubercle on the talar neck, provide for the "locking" of the ankle joint in full dorsi-flexion. This would permit resting in a relaxed squatting position, with the ankle fully dorsi-flexed, and it would also make possible sudden and rapid leaping movements from this position of rest.

The posterior position of the basal tubercle of the calcaneum and the backward extension of the main facet for the talus appear to indicate that if *Proconsul* occasionally raised itself on its hinder extremities like the modern Pongidae, it was able to throw its weight back more towards the heel, and thus to balance itself in the erect posture more effectively. The possible implications of this in relation to the subsequent development of a bipedal gait are sufficiently obvious. It is not suggested here that any of the early Miocene hominoids from East Africa necessarily bear a relationship, direct or indirect, to the ancestral stock from which the Hominidae originated. But at least it seems probable from the conformation of the talus and calcaneum that the tarsal pattern of the human foot might have been more readily derived from that of *Proconsul* than from that characteristic of any of the modern large anthropoid apes.

The inference from the talus and calcaneum that *Proconsul* was a creature adapted for active quadrupedal progression is in harmony with the evidence of the femur for, as we shall see, its straight slender shaft, as well as certain details of the lesser trochanter and the neck of the bone, implies a lightness of build and an agility comparable with the large cercopithecoids rather than with the modern large apes. The talus by itself, apart from its size, conforms much more closely to the cercopithecoid talus than to that of the modern Pongidae.

In addition to the large tali described above, two much smaller tali (surface specimens) were found in a well-preserved condition on Rusinga Island (Pl. 9, figs. 71, 72). These bones reproduce on a smaller scale the features of the large tali, and they show no distinguishing features by which they can be differentiated from the tali of the larger modern cercopithecoid monkeys (e.g. the langurs). Thus, it is not possible to say whether they belong to one of the smaller hominoid species found in the same region, or to a Miocene cercopithecoid (? *Mesopithecus*). The dorsal and plantar aspects of the bones are illustrated in Pl. 9, figs. 71, 72, and the following are some of the main dimensions:—

	Total length	*Max. width of articul. head*	*Max. ht. of head*	*Length along median axis of sup. facet*	*Width of ant. margin of sup. facet*	*Width of post margin of sup. facet*	*Ht. of lat. malleolar facet*
B 2 . . .	32	14	11	17	13	8	14
B 3 . . .	30	13	10	15	11	7	12

Femur (Pl. 9, fig. 69, and text-fig. 23).—Among a number of fossilized remains discovered by the late Archdeacon Owen in 1933 on Maboko Island, and sent by him to the British Museum, were fragments of limb bones referable to a large primate. They include the greater part of a right femur, the upper extremity and shaft of a left femur, the shaft of a left humerus, and part of a right clavicle. It is highly probable that these bones belong to the same individual. Unfortunately, no precise information

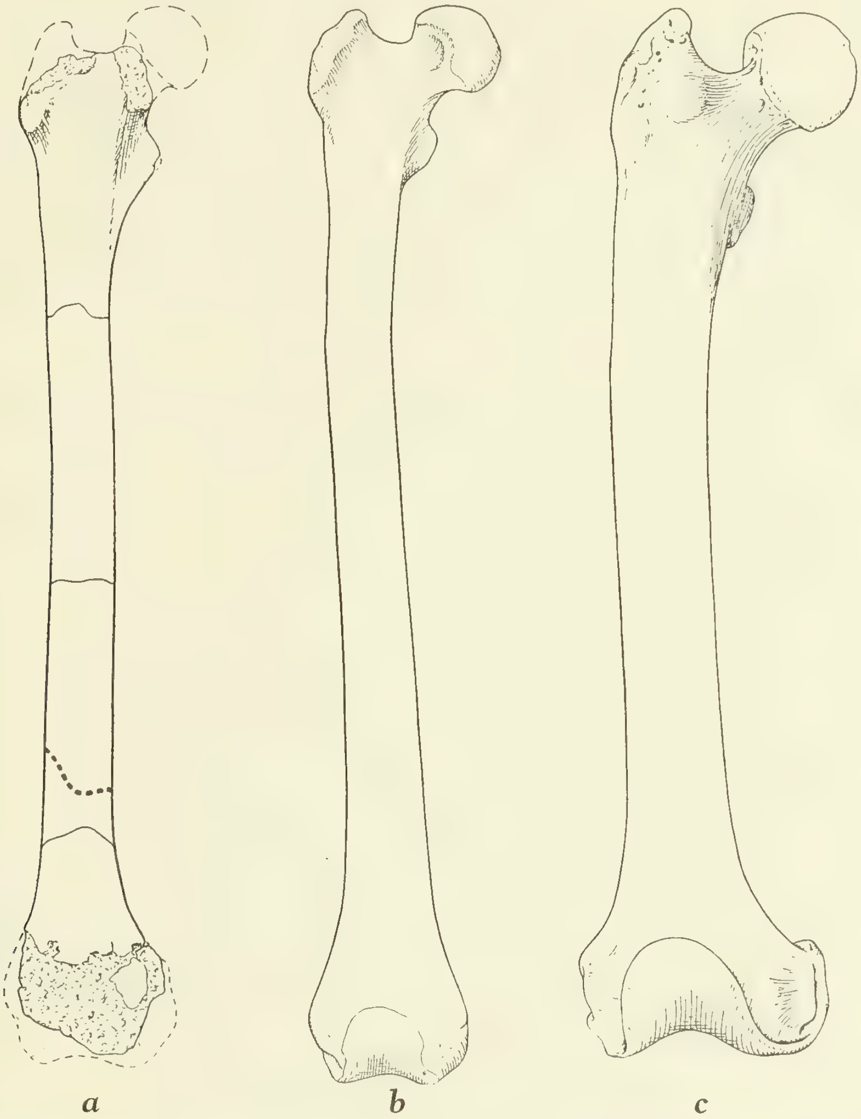

FIG. 23. A. The right femur of ? *Proconsul* viewed from the anterior aspect. The head and greater trochanter have been drawn in from the upper extremity of the left femur in which these parts are practically intact. The interrupted line indicating the contour of the lower extremity is entirely conjectural. The interrupted line across the lower third of the shaft indicates the position here of an angulation in the fossil specimen for which correction has been made in the drawing. B. Femur of *Dryopithecus* (*Paidopithex*), drawn from a cast. C. Right femur of a male chimpanzee. All drawings have been made to the same scale—half natural size.

is available regarding the exact position of the site. Although their documentation is thus incomplete, the characters of the bones themselves are of sufficient interest to merit a general description of their main morphological features.

In the absence of associated teeth, it must remain doubtful to which genus of early Miocene primates the Maboko femora, humerus and clavicle belong. *Mesopithecus* and *Limnopithecus* can be definitely excluded because of the disparity in relative size. On the other hand, the only large primates of conformable size known from the Miocene deposits in this area are representatives of the genus *Proconsul*, and the species *Sivapithecus africanus*. Because of the rarity of remains of the latter species, their allocation to the genus *Proconsul* seems more likely, and this is the identification which we propose to adopt here. The straightness, slenderness, and relatively small articular extremities of the femora, compared with a male chimpanzee (in which the adult femur is of an equivalent total length), indicate a creature of comparable linear dimensions but of much lighter build. Presumably, also, it was much more active and agile.

Apart from a negative process of exclusion, the determination of the primate character of the femora depends on positive characters such as the straightness and slenderness of the shaft in relation to its absolute length, the length, obliquity, and contour of the neck, the shape of the greater trochanter, and the absence of a third trochanter. The right femur is practically complete except for the head and neck of the bone, the free part of the greater trochanter, and the condyles and articular surface of the lower extremity. Near its lower end, the shaft has become slightly angulated at the site of a post-mortem fracture (the site of this angulation is indicated in text-fig. 23 by an interrupted line). The left femur is represented by the upper extremity in which the head and neck and the greater trochanter are almost intact (Pl. 9, fig. 69), and by the middle and lower portions of the shaft.

The maximum length of the femur, as estimated from the bone of the right side, after reconstructing the head and neck by reference to the bone of the left side, correcting for the angulation of the shaft, and reconstructing the lower extremity, is approximately 285 mm. The reliability of this estimate depends on the accuracy of the reconstruction of the lower extremity (as will be apparent by reference to text-fig. 23), but since a considerable portion of the epiphysial region is present, there can hardly be an error of more than 15 mm. either way. At the middle of the shaft, the transverse diameter on each side is 17 mm. and the antero-posterior diameter 18 mm.

The surface of the shaft is generally smooth and even. It lacks a narrow, sharply defined linea aspera, the area for the attachment of muscles in this region being represented by a relatively broad and smooth zone about 8 mm. wide in the middle of the shaft outlined by faint ridges. In this feature, the femur resembles that of the modern large apes. Viewed from in front, the shaft appears practically straight; from the side it is seen to have a very slight forward convexity.

The upper extremity of the left femur is shown in Pl. 9, fig. 69. The head is almost spherical, measuring 22·6 mm. in vertical and 23·0 mm. in antero-posterior diameter. There is a well-marked fovea a little below its central point. The neck is relatively slender, and sharply constricted from the articular margin of the head of the femur. It makes an angle of approximately 130° with the axis of the shaft.

About half way along the posterior aspect of the neck, near its upper margin, is a small circumscribed tubercle. Such a tubercle is commonly found in the femora of Old World monkeys, particularly the langurs. It is not normally present in the recent large anthropoid apes, but may occasionally be found in an indistinct form in the gibbon. The significance of this tubercle is obscure. Dissections of macaque monkeys show that it does not serve for the attachment of any ligamentous structure, but it is commonly related to a local extension outwards of the articular surface and this, in turn, is related to a thickening of the capsule of the hip-joint formed by a strong development of the ischio-femoral ligament. A tubercle of very similar proportions is present in the neck of the Eppelsheim femur and is mentioned by Dubois (1897) in his account of that fossil. It has also been described as an occasional occurrence in modern human femora by Sauser (1935), who seeks to associate it with hill-climbing activities, suggesting that with the hip-joint in a flexed position much of the body weight is sustained by the ischio-femoral ligament. If this is so, the absence of the tubercle in the modern large apes (in contrast to its presence in the Cercopithecoidea) is presumably correlated with the development of a type of arboreal specialization which involves no habitual strain on the hip-joint. In monkeys, on the other hand, it may be related to the necessity for stabilizing and fixing the hip-joint in a flexed position from which rapid leaping or springing movements can be initiated. A tubercle of very similar appearance, it may be noted, is also present on the femoral neck of active carnivores, such as the cheetah.

The greater trochanter is of moderate size, the tip being below the level of the summit of the articular head. Anteriorly, it is demarcated from the upper end of the shaft by a well-defined ridge. The eminence corresponding to the upper tubercle of the trochanteric line of the human femur (which receives the attachment of the upper band of the ilio-femoral ligament) is but feebly marked, in contrast to its strong development as a rounded boss in modern apes and Old World monkeys. There is no trochanteric line, the anterior surface of the bone between the neck and the shaft being quite smooth. The lesser trochanter projects medially as a flattened flange of bone with a sharp lower border, resembling in its shape and relative size that of the Old World monkeys rather than the modern large apes. At its summit is a flat oval bursal facet of a type which is a common cercopithecoid feature. The upper end of the gluteal ridge is conspicuous, but not sufficiently so to be designated a " third trochanter".

The shaft of the femur widens gradually at its lower end. The popliteal surface is smooth and very slightly convex. The maximum width of the lower extremity can only be approximately estimated. It is certainly much less proportionately to the width of the shaft than in the modern large apes.

The primate femora found on Maboko Island make an interesting comparison with the Eppelsheim femur discovered in Lower Pliocene deposits in 1820, described by Pohlig (1895) under the name of *Paidopithex rhenanus*, assumed by Schlosser (1902) to belong to *Dryopithecus*, and regarded by Dubois (1897) as the femur of a large gibbon which he called *Pliohylobates*. As will be seen by reference to text-fig. 23, the Eppelsheim femur is remarkably similar in its general proportions to the Maboko femora. In total length they are closely comparable, and in details such as the relative size of the articular head, the contour of the neck, the presence of a tubercle on the posterior aspect of the latter, the relative size of the trochanters, the degree of development of the upper end of the gluteal ridge, the cross-sectional outline of the middle of the shaft, and the dimensions of the popliteal portion of the shaft, they are almost identical. In the Eppelsheim femur the lower articular extremity is preserved. Its broad, shallow patellar surface and divergent condyles are definitely anthropoid ape characters. There are two features in which the Eppelsheim femur differs from the

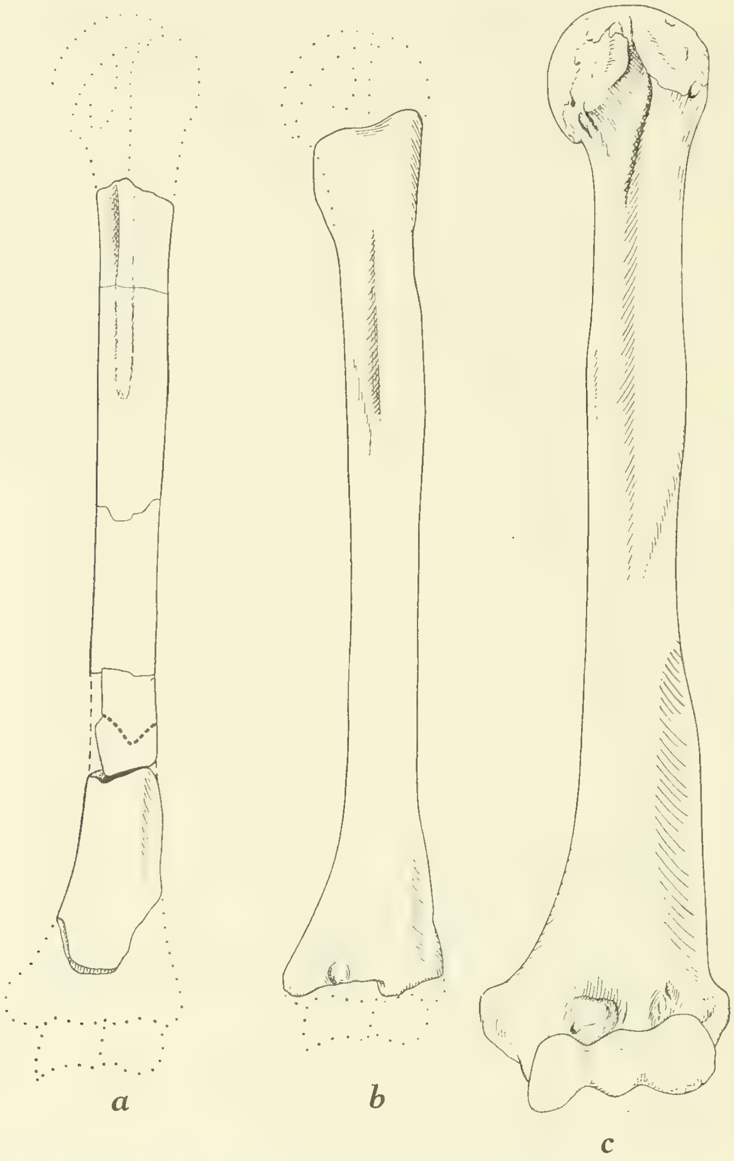

FIG. 24. A. Shaft of left humerus of ?*Proconsul* viewed from the anterior aspect. The interrupted line across the lower half of the shaft indicates the position here of an angulation in the fossil specimen for which correction has been made in the drawing. The dotted lines indicating the contours of the upper and lower extremities are entirely conjectural. B. Shaft of the left humerus of *Dryopithecus fontani* viewed from the anterior aspect (drawn from a cast). C. Left humerus of a male chimpanzee. All specimens have been drawn to the same scale—half natural size.

Maboko femora—the lesser trochanter forms a more localized rounded boss and is less flange-like (thus resembling more closely that of the modern large apes), and the lower extremity is, perhaps, slightly broader.

The assumed hylobatine nature of the Eppelsheim femur rests on general comparisons only, but no other remains of a gibbon of such a large size have ever been found in the Upper Miocene or Lower Pliocene deposits of Europe (or, indeed, anywhere else). In fact, the only hominoids of comparable size from European deposits are various species of *Dryopithecus*.

In 1932 a portion of the upper end of a large primate femur was found on Rusinga Island close to the fragment of a mandible (C.M.H.5) of *Proconsul nyanzae*, and at the same site where the dentition (C.M.H.3 and 4) of this species, and also an immature mandible (C.M.H.110), were found. This very incomplete specimen is shown in Pl. 9, fig. 70. It is similar to the Maboko femora, but slightly larger. The lesser trochanter is a relatively more circumscribed eminence, and is situated at a lower level in relation to the head and neck of the bone. The diameter of the articular head is 26·5 mm. in vertical and antero-posterior directions. On the posterior aspect of the neck is a small tubercle towards which a local extension of the articular surface can be discerned.

Humerus (text-fig. 24).—With the remains of the two femora from Maboko was also found the greater part of the shaft of a left humerus, broken by transverse fractures into five pieces which fit together accurately. There is, however, a slight angulation of the shaft at one point. This angulation has been corrected in the illustration shown in text-fig. 24, where its position is indicated by a dotted line, the correction being readily made by aligning longitudinal cracks on the surface of the bone.

At its broken extremity, the upper end of the shaft is beginning to widen out as it approaches the region of the humeral neck, and it shows here a well-defined bicipital sulcus. The lateral lip of the sulcus is roughened, and prolonged down into a slight forward convexity at the middle of the shaft—the lower part of the deltoid insertion. In this forward convexity of the shaft, the humerus shows a striking resemblance to that of the cercopithecoid monkeys rather than the modern anthropoid apes. There is no other impression on the bone marking the attachment of the deltoid muscle, and no spiral groove is present.

The lower end of the shaft shows the middle part of the upper margin of the olecranon fossa. Just above this level, the posterior surface of the bone is flattened and slightly concave, and the supinator ridge is relatively small. In text-fig. 25 are shown the outlines of cross-sections through the lower end of the humeral shaft (2·0 cm. above the upper margin of the olecranon fossa) in *Dryopithecus fontani* (from the Middle Miocene of Haute Garonne), a male chimpanzee, a modern European male, and the present specimen from Maboko. They serve to emphasize the comparatively weak development of the supinator ridge in the fossil bones. This ridge provides attachment for the m. brachio-radialis, which is often powerfully developed in the modern large apes in relation to their brachiating habits.

The total length of the humerus as estimated from the reconstruction shown in text-fig. 24 is about 280 mm. The accuracy of this estimate depends, of course, on the reconstruction of the extremities. However, the upper margin of the olecranon fossa below, and the incipient increase in the width of the shaft at its upper broken extremity are believed to provide useful information on which to base the reconstruction. The proportions of the humerus conform well with those of the femora also found on Maboko Island, and confirm the inference that the creature to which they belonged must have been of the same general size as the chimpanzee, but of much lighter build.

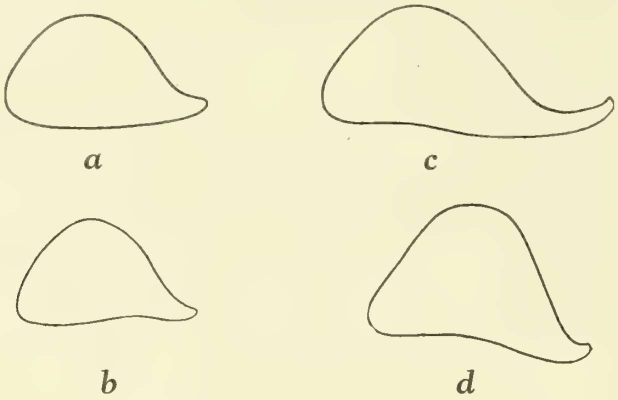

Fig. 25. Transverse sections through the lower end of the shaft of the humerus (taken 2 cm. above the upper margin of the olecranon fossa) of (a) *Dryopithecus fontani*, (b) ?*Proconsul*, (c) male chimpanzee, (d) *Homo sapiens*. Natural size.

The similarity (in general proportions) of the Maboko humerus to that of the European species, *D. fontani*, of Middle Miocene date is striking (text-fig. 24). In his original description of this specimen in 1856, Lartet noted the rounded, slender character of the shaft and compared it in this respect with the gibbon's humerus.

Clavicle.—Two specimens appear to be portions of hominoid clavicles, in each case consisting of approximately the middle third of the bone and part of the lateral extremity. One clavicular fragment (text-fig. 26) was found on Maboko Island in association with the humerus and femora; it is of correspondingly slender proportions.

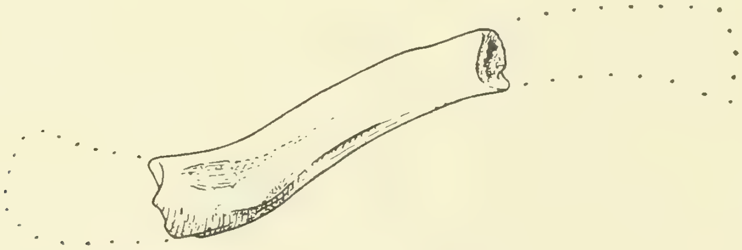

Fig. 26. Fragment of the middle part of the clavicle of ? *Proconsul* viewed from below. Natural size. The outlines of the extremities of the bone are tentatively indicated.

The maximum diameter of the bone at the centre of the estimated total length is 9 mm. The conoid tubercle is small, and there are no other irregularities on the surface of the bone.

The other clavicular fragment (604, R.106) was found on Rusinga Island. It is part of a much larger bone; the maximum diameter at the centre of its estimated total length is 15 mm. The conoid tubercle is relatively more prominent than in the smaller specimen, and from it a strong trapezoid ridge extends antero-laterally. The under surface of the distal extremity lacks the marked concavity which is characteristic of the clavicle of the modern large apes. The markings for the attachments of the trapezius and deltoid muscles are strongly developed, as is also the posterior lip of the groove for the subclavius muscle. In its general bulk, this clavicle compares well with that of a large male gorilla. Possibly it is attributable to *Proconsul major*, of which the jaws and teeth reach gorilline dimensions.

IX. THE MIOCENE HOMINOIDEA OF EAST AFRICA IN RELATION TO THE EVOLUTION OF THE PRIMATES

Undoubtedly one of the most surprising features of the palaeontological material from the Lower Miocene deposits of East Africa is the evidence it provides that, at so early a time, a profusion of hominoid types had already come into existence. This diversity had been previously indicated by Hopwood (1933*a*). It has been still further emphasized by later discoveries. In the smallest of the fossil apes, *Limnopithecus legetet,* the dimensions of the teeth approach closely to the lowest limit of variation in the smaller species of the modern gibbons. At the other extreme, the dimensions of the lower molars in *Proconsul major* approximate to the average of those of male gorillas. Between these two extremes there is a series of types which are rather closely graded in size, and which, indeed, at first presented some difficulty in attempts to classify them. These close gradations suggest that in East Africa during the early Miocene period, the evolutionary development of the Hominoidea was proceeding at a rather rapid rate, resulting in a number of diverse types which perhaps had not yet achieved complete genetic segregation. Even were the latter the case, however, the diversity of types still remains impressive when account is taken of their geological antiquity, for, although small hominoids, in some respects rather similar to *Limnopithecus*, were already in existence in the preceding Oligocene period, the large fossil apes (Dryopithecinae) known from other parts of the world are of considerably later date (Middle Miocene to Lower Pliocene).

Apart from two specimens of possible hominoids from the Upper Eocene of Burma, the doubtful *Pondaungia cotteri* (Pilgrim, 1927) and the much more suggestive *Amphipithecus mogaungensis* (Colbert, 1937), the only fossil hominoids of earlier or equivalent age known prior to the discovery of early Miocene primates in East Africa had been found in Egypt. This material has been reported by Schlosser (1911), and Osborn (1908) from Oligocene deposits in the Fayum and by Fourtau (1920) from the Lower Miocene (Burdigalian) horizon of the Moghara escarpment. There is some doubt, however, whether all these fossils can be legitimately assigned to the Hominoidea.

Fourtau's descriptions and photographic illustrations are not adequate to permit a critical examination of his conclusions. The small mandibular fragment, with the much worn P $\overline{4}$ and M $\overline{1}$–$\overline{3}$, which he attributes to a new genus and species, *Prohylobates tandyi,* does not seem to show very definite hominoid characters. Indeed, so far as can be made out from the photograph, the molars appear to be more cercopithecoid in their cusp pattern. His other new type, *Dryopithecus mogharensis,* based on two incomplete mandibular fragments, is equally dubious. The lower molars are considerably smaller than in any other known representative of the Dryopithecinae; they are stated to have a distinct internal cingulum.

The fossil material described by Schlosser, and excellently illustrated, includes

Parapithecus, *Propliopithecus*, and *Moeripithecus*. The first two genera require special consideration in this discussion, since in their lower molar structure they show undoubted affinities with *Limnopithecus*. *Moeripithecus* is represented only by the first and second lower molars, each of small size (M $\overline{1}$ length 5 mm., M $\overline{2}$, 5·5 mm.), and each with a length-breadth index of 100. In the marked reduction of the hypoconulid, in the disposition of the four main cusps and the separation of the front from the back pair by rather deep sulci on the sides of the crown, and in the strong development of the crest between the protoconid and metaconid, these teeth suggest a definite approximation to the cercopithecoid type, and the points made by Remane in his provisional assignment of *Moeripithecus* to the Hylobatinae seem to be equally favourable to such an interpretation.

The Oligocene genus *Apidium*, defined by Osborn on the basis of a mandibular fragment with P $\overline{1}$ and M $\overline{1}$–$\overline{3}$, appears to show more definite cercopithecoid characters, and, indeed, is now generally classified with the Cercopithecidae (Abel, 1931; Simpson, 1945). The regression of the hypoconulid (particularly in M $\overline{2}$), the disposition of the four main cusps, and the elongated talonid in M $\overline{3}$, support such a view. Gregory (1922) has expressed the opinion that this genus represents an intermediate form linking the *Necrolemur* phase of primate evolution with the lower Pliocene cercopithecoid, *Oreopithecus*. The primitive status of *Apidium* is shown by the rudiment of the paraconid which still persists on the first molar.

Of the fossil material from Egypt mentioned above, it is probable that only *Parapithecus* and *Propliopithecus* can be considered as early representatives of the Hominoidea. Their claim to hominoid status depends mainly on the characters of the lower molars, which strongly suggest hylobatine affinities. The resemblances which these teeth show to those of *Limnopithecus* are sufficiently close to demand special consideration here. The *Limnopithecus* material from East Africa includes at least two separate species of which the smaller, *L. legetet*, is in several respects more primitive than the larger, *L. macinnesi*, and thus approximates more closely to the Oligocene genera.

Both Hopwood (1933*a*) and MacInnes (1943) recognized that the morphological characters of the lower molars of *Limnopithecus* are adequate for placing this genus provisionally in the subfamily Hylobatinae. Hopwood argues that *L. legetet* shows more " advanced " characters than *Hylobates* in the cusp pattern of the deciduous molars, and particularly in the presence in the posterior deciduous molars of a hypoconulid. The latter is said to be absent in the corresponding milk tooth of *Hylobates*, but this is evidently not always the case, for a trace of it is certainly to be discerned in a specimen of *H. mulleri* in the Department of Anatomy at Oxford. The lower deciduous teeth of a gibbon figured by Gregory (1922, fig. 295) show a well-defined hypoconulid on Dm $\overline{4}$. Lastly, Remane (1921) in his description of the milk dentition of *Hylobates* notes that the hypoconulid (" mesoconid ") is median in position and occasionally much reduced. In any case, however, the absence of the hypoconulid in the second milk molar is more likely to be a secondary feature due to the loss of what must be regarded as a very primitive dental character of the Primates. The other characters in which *L. legetet* is evidently less specialized than *Hylobates* are (1) the relatively small and more brachydont canine, (2) the less sectorial form of P $\overline{3}$, the crown is less compressed laterally and the enamel shows no tendency to extend down on the anterior root, (3) the lower molars increase progressively in length from the first to the third, (4) the cusps of the lower molars are of approximately equal size, except for a reduction of the entoconid in M $\overline{3}$, whereas in *Hylobates* the metaconid tends to hypertrophy and the hypoconid may be unusually reduced in M $\overline{2}$ and M $\overline{3}$, (5) the hypoconulid is more central in position, (6) the cusps of P $\underline{3}$ are of almost equal size, whereas in *Hylobates* the buccal cusp is longer and more pointed in correspondence with the more sectorial form of P $\overline{3}$, (7) the trigon in the upper molars is smaller in proportion to the occlusal surface as a whole, (8) the upper molars have a well-defined internal cingulum, (9) the lower molars have a well-defined external cingulum, (10) the talonid of M $\overline{3}$ is produced back into a narrowed heel, (11) the cusps are separated by deep intervening sulci, whereas in *Hylobates* they tend to be united along the margins of the crown by interconnecting crests—particularly evident in the prominent crista transversa anterior, which is commonly present between the protoconid and metaconid, (12) the symphysial region of the mandible is narrower, (13) the mandible as a whole is of more robust build.

The resemblance of the lower dentition of *L. legetet* to that of *Propliopithecus* is close. It is particularly noticeable in the shape and proportions of the molar cusps, in the lack of prominent crests connecting them, in the weak development of the posterior fovea, and in the presence of a well-developed external cingulum. In *Propliopithecus*, the occlusal aspect of M $\overline{1}$ and M $\overline{2}$ has a more rectangular contour. The hypoconid appears to be relatively larger than in *Limnopithecus*. In M $\overline{1}$, the crown is broader, the hypoconid is more nearly opposite the entoconid, and the hypoconulid is interposed between these two cusps, appearing to thrust them apart, so that the transverse distance between the entoconid and hypoconid is conspicuously greater than the distance between the protoconid and metaconid. This relative disposition of the cusps is distinctly reminiscent of the tuberculo-sectorial molars of lower primates, in which the talonid basin is much wider than the trigonid (e.g. in tarsioids, and also in the Eocene *Amphipithecus*). A similar forward position of the hypoconulid in M $\overline{1}$, associated with a widening of the interval between the hypoconid and entoconid, is found in *Parapithecus*. It may also occur in *L. legetet* (e.g. in the holotype), but in this species the hypoconulid is more commonly placed well behind the level of the hypoconid. The anterior premolar in *Propliopithecus* has a much less pronounced sectorial form; it has a conical shape and is more rounded in cross-section, and the talonid is represented only by a slight excavation on the posterior aspect of the single cusp. The tooth is, properly speaking, unicuspid, for the lingual cusp (metaconid) is represented by no more than a slight thickening of the internal cingulum. The posterior premolar of *Propliopithecus* differs from that of *L. legetet* in being relatively shorter and having a less extended talonid. The canine in *Propliopithecus* is evidently more brachydont and spatulate. In many of these characters, *L. legetet* appears to occupy a morphological position which is intermediate between *Propliopithecus* and *Hylobates*.

In comparison with *Pliopithecus antiquus* (of Upper Miocene date), the mandible of *L. legetet* has similar general dimensions, but the molar and premolar teeth are smaller. So far as can be judged from casts and drawings, the external cingulum is somewhat less pronounced in *Pliopithecus* (particularly at its anterior extremity), the hypoconulid is relatively smaller in M $\overline{1}$ and M $\overline{2}$ and is displaced laterally more in line with the protoconid and hypoconid, and the anterior lower premolar is less compressed laterally. The lower canine in *Pliopithecus* appears to be somewhat more specialized in its relatively greater height and in the development of a rather pronounced secondary cuspule on the heel. In the size and details of the lower molars, *L. legetet* shows a closer resemblance to *Propliopithecus* than to *Pliopithecus*, but it approaches the latter more nearly in the relative size of the canine and the characters of P $\overline{3}$.

The mandible and lower teeth of *Parapithecus* are considerably smaller than those of *L. legetet*, and the canine and premolars show much more primitive features. On the other hand, the cusp pattern of the molars is closely comparable, and the position of the protoconid relative to the metaconid in M $\overline{1}$ is much the same. However, the external cingulum on the molars is poorly developed (according to Schlosser it is only distinct at its anterior and posterior extremities), and herein *Parapithecus* contrasts rather strongly with *Propliopithecus*, *L. legetet* and *Pliopithecus*.

If all the characters of these fossil species are taken into account, one may construct an approximate morphological sequence leading from *Parapithecus* through *Propliopithecus*, *Limnopithecus legetet*, and *Pliopithecus* to *Hylobates*. It is not, of course, suggested that this represents an actual linear evolutionary series, and undoubtedly there are certain features (some of which are perhaps of minor importance) which may be adduced as contrary arguments. For example, the degree of development of the external cingulum in *Propliopithecus* and *L. legetet* is probably a primitive feature which, in *Parapithecus*, has undergone some retrogression. The anterior lower premolar in *Pliopithecus* appears to be a little less specialized than it is in *L. legetet*. The last molar in *Propliopithecus* is slightly shorter than the second molar, a relationship (presumably secondary) which is not found in any of the specimens of *Limnopithecus* so far discovered. Broadly speaking, however, the sequence appears to illustrate the following changes. There is evidently a progressive widening of the incisor region of the mandible, commencing with the V-shaped divergence of the horizontal rami from the narrow pointed symphysis in *Parapithecus* which, as previous authors have noted, gives the jaw a somewhat tarsioid appearance. The canine increases in height, becomes more curved, and develops a sharp posterior border. The anterior lower premolar becomes more sectorial. The lower molars increase in relative length and finally lose the external cingulum. Their cusps tend to become interconnected along the margins of the occlusal surface by more or less well-defined crests, and the posterior fovea becomes more distinct. The main "paired" cusps tend to become placed more directly opposite each other. The hypoconulid becomes reduced in M $\overline{1}$ and M $\overline{2}$ and displaced laterally to the median axis of the crown.

In *L. macinnesi*, some of these features have already advanced further than in the smaller species of *Limnopithecus* and, indeed, in the lateral compression of P $\overline{3}$ this species appears to have surpassed in specialization even the modern Hylobatinae. The cusp pattern of the lower molars, however, shows primitive characters in the relative sizes of the main cusps, in the forward position of the protoconid in M $\overline{1}$, in the less strong development of the crista transversa anterior, in the more pronounced development of the hypoconulid in M $\overline{2}$ and M $\overline{3}$, and in the relative length of M $\overline{3}$. In general, the molars resemble those of *Symphalangus* more closely than *Hylobates*, for in the latter the trigonid portion of the crown, the posterior fovea, and the hypoconulid have undergone greater reduction, perhaps resulting from a general compression of the molar series related to a secondary reduction in their size. According to the observations of Schultz (1933), the tooth row of *Hylobates* also tends to become shortened by the gradual elimination of the last molars, as in *Ateles* and *Homo*. The sharp dagger-like upper canines of *L. macinnesi* are directly associated with the advanced sectorial development of $\mathrm{P}\,\overline{3}$, and also with the pronounced development of the buccal cusp of $\mathrm{P}\,\underline{3}$; in these features, as well as in the reduction of the external cingulum in the molars, a closer approach (in comparison with *L. legetet*) is made to the modern gibbon. On the other hand, *L. macinnesi* resembles *Pliopithecus* in certain features, particularly in the more primitive characters of the lower molars enumerated above, and in the morphology of the upper molars. According to Hofmann's (1893) illustrations and measurements, the upper molars of *Pliopithecus* are very similar to those of *L. macinnesi* in their size and proportions (see Table 11), and in the development of the internal cingulum, which, however, is not so strongly developed, neither does it show any evidence of elaboration by a fine beading such as is present in the East African species. The lower canine tooth and $\mathrm{P}\,\overline{3}$ of *Pliopithecus* are clearly less specialized. In considering the relationship of *L. macinnesi* to *L. legetet*, it seems not a little remarkable that in the early Miocene period of East Africa there already coexisted two hylobatine species of contrasting types, the one primitive and the other advanced. They appear to confirm the suggestion that, at that time, hominoid evolution was proceeding at a rather rapid rate.

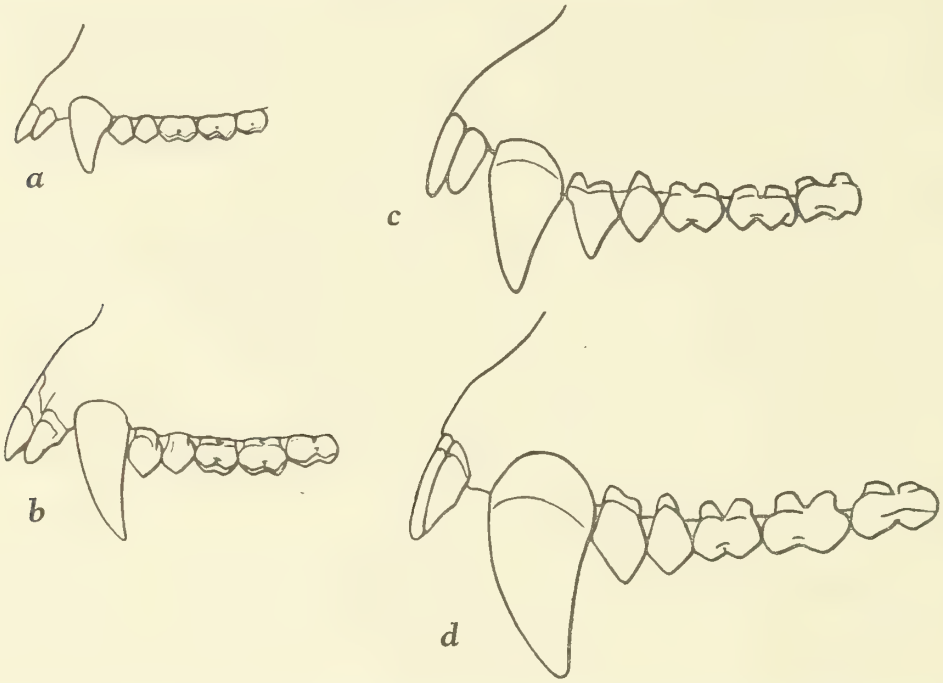

FIG. 27. Graphic reconstructions of the upper dentition of (a) *L. legetet* (drawn by reference to specimens S.59, S.120, S.101), (b) *L. macinnesi* (drawn by reference to specimens 545, 1947, and S.57), (c) *P. africanus* (drawn by reference to the holotype M.14084), (d) *P. nyanzae* (drawn by reference to the holotype C.M.H.2). Natural size.

The true position of *Parapithecus*, *Propliopithecus*, and *Pliopithecus* in the evolutionary history of the modern gibbon cannot be decided until more complete skeletal material of these genera becomes available. Features suggestive of a slight degree of specialization in the mandible and lower dentition of *Pliopithecus antiquus* have been adduced by Pilgrim (1915), Remane (1921), and others, as arguments against the idea of an ancestral relationship, but we are inclined to agree with Gregory (1916) and Abel (1931) that this evidence is by no means strong enough to justify a definite statement. However, the discovery of advanced types of apparently hylobatine affinities in the Miocene deposits of Kenya renders it less probable that the much later *P. antiquus* of Europe is itself to be regarded as the forerunner of the modern gibbons of East Asia. In this connection, it may be noted that Pilgrim (1927)

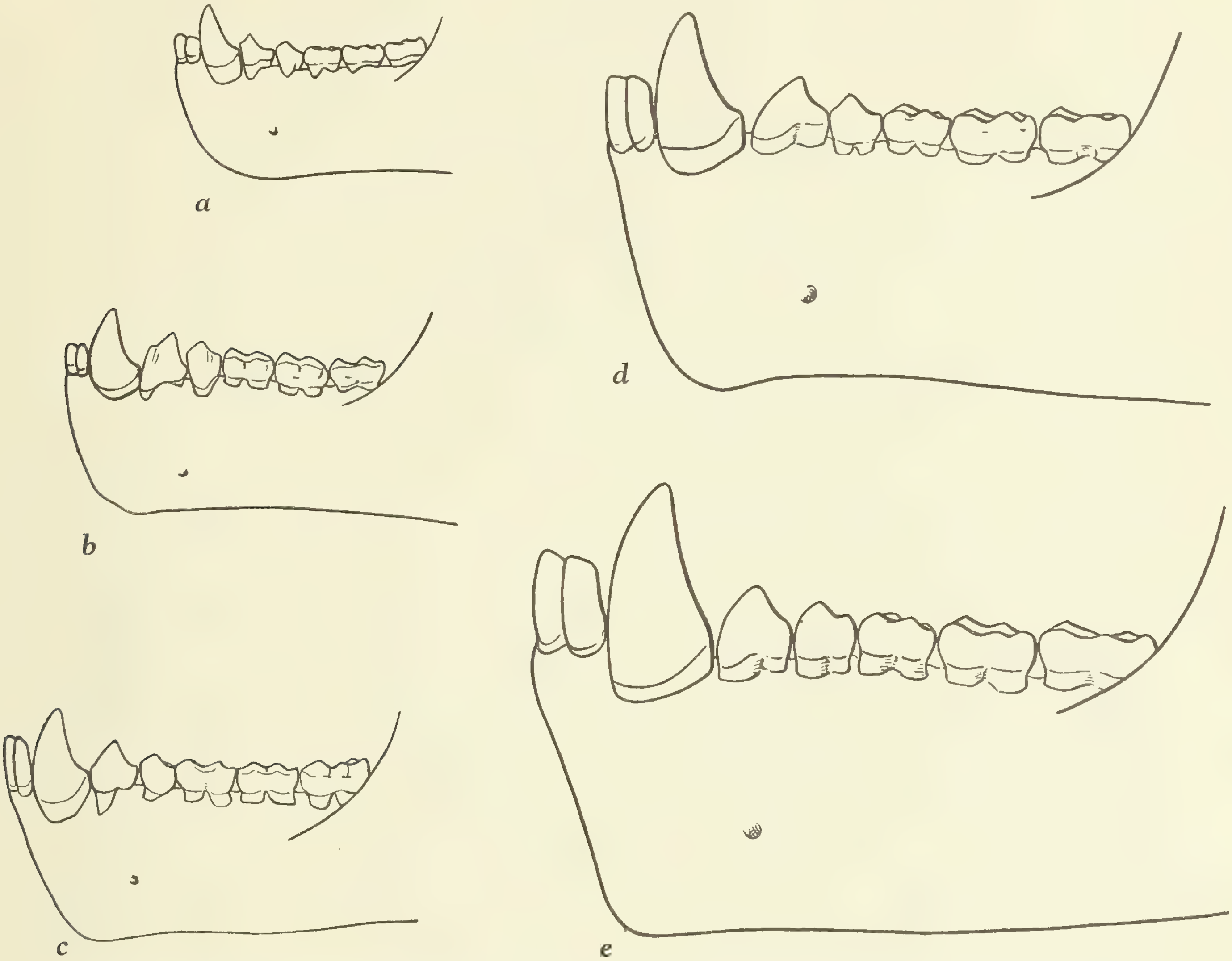

FIG. 28. Graphic reconstructions of the lower dentition of (a) *L. legetet* (drawn by reference to specimens S.13 and C.M.H.105), (b) *L. macinnesi* (drawn by reference to specimens 710, 1947, and S.29, 1947), (c) *P. africanus* (drawn by reference to specimens C.M.H.102, 559, and R.1948, 50), (d) *P. nyanzae* (drawn by reference to specimens C.M.H.4, S.28, 1947, Rs.106, and the Koru mandible), and (e) *P. major* (drawn by reference to specimens S.1, 1947, and S.80, 1947). Natural size.

described a species, *Hylopithecus hysudricus*, probably derived from the Nagri horizon of the Siwalik formations (lower Pliocene), which, he suggested, might represent a precursor of the recent Hylobatinae. Unfortunately, the specimen on which this species was based consists only of a lower molar (probably M $\overline{2}$) which is much worn. However, it resembles *L. macinnesi*, not only in its dimensions (antero-posterior diameter 8·8 mm., transverse 7·3 mm.), but also in the disposition of the cusps and the presence of the posterior fovea. The external cingulum is also stated to be absent. The only other record of *Pliopithecus* in Asia is the species, *P. posthumus*, described by Schlosser (1924) on the basis of an isolated and worn upper third molar from Ertemte in Southern Mongolia (Middle Pliocene, according to Young, 1934). Even if the dimensions of this tooth preclude a close relationship to the modern gibbon, at least it provides evidence, as Abel (1931) pointed out, that the Hylobatinae were represented in East Asia in late Tertiary times.

So far as the East African fossils are concerned, one conclusion seems certain, namely that, at least on the basis of dental structure, *Limnopithecus* is quite closely related to *Propliopithecus* and *Pliopithecus* and may be provisionally included in the subfamily Hylobatinae. It is also clear that, in spite of their smaller size, the cusp pattern of the lower molars of *Parapithecus* indicates a not very distant relationship to *Propliopithecus* and *L. legetet*. *Limnopithecus* thus represents a progressive, early Miocene, development of the *Parapithecus-Propliopithecus* sequence, whatever may be its true relationship to the much later *Pliopithecus* or to the modern gibbon.

So far as can be judged by the quantity of their fossil remains which have come to light during recent years, the anthropoid ape population in East Africa during the early Miocene period was mainly composed of representatives of the genus *Proconsul*.* As we have seen, this genus contained species of widely different size, ranging from *P. africanus* which, in the dimensions of the skull, was intermediate between the large modern gibbons (*Symphalangus*) and the pigmy chimpanzee (*Pan paniscus*) to *P. major* which, in the size of the mandible and lower dentition, is most closely paralleled among the recent large apes by the gorilla. In all these forms, which were presumably contemporaneous, or at least approximately so, the basic features of the dentition are similar, and the gradations of size are so close that, on the basis of the lower dentition alone, it would be a matter of some difficulty to determine the limits between one species and another. This is particularly true of *P. africanus* and *P. nyanzae*. However, quite apart from the dimensions of the teeth, the differences of detail in the cusp pattern of the upper dentition seem to warrant a specific distinction (see p. 54). The discovery of the skull of *P. africanus* with a practically complete mandible has served to confirm this conclusion, for the form and proportions of the mandible are very different from those of *P. nyanzae*, as may be seen by reference to the comparative drawings in text-fig. 10. In the absence of more complete material, the distinction between *P. nyanzae* and *P. major* is perhaps not so obvious. However, the contrast in absolute dimensions of the mandible and lower teeth is impressive. For example, the length of the largest second lower molar of *P. major* exceeds that of the equivalent tooth in the 1942 mandible of *P. nyanzae* by no less than 147 per cent., and thus actually surpasses the range of variation for M $\overline{2}$ in the whole of any one genus of the modern large apes (according to Remane's data). Reference to text-figs. 9A and 18, showing mandibles of the two species viewed from above, further serves to emphasize this difference in size.

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* Reference should be made here to Hopwood's genus *Xenopithecus*, based on two much worn upper molar teeth (Hopwood, 1933). We have not been able to identify any specimens in our material which we can attribute to this genus. Either *Xenopithecus* is a rare type of anthropoid ape in the early Miocene of East Africa or, as seems more probable, the small differences in cusp pattern of the upper molars are merely representative of an unusual variant within the species *Proconsul africanus*.

[Professor le Gros Clark was kind enough to let me examine all the material. I have no doubt that his conclusions are correct and that *Xenopithecus* is synonymous with *Proconsul*. The former has page priority over the latter, but this is not true priority, and the name *Xenopithecus* should be abandoned in favour of the better-known name *Proconsul*. A. T. H.]

The distinctive features of the dentition of *Proconsul* are to be found in the maxillary rather than in the mandibular teeth, and the main characteristic of the former is undoubtedly the strong development in the molars of the internal cingulum and, to a lesser extent, of the anterior and posterior cingula. In some cases there are also rudiments of an external cingulum. The internal cingulum in the smaller species of *Proconsul* forms a projecting shelf which appears to extend the occlusal surface of the tooth, whereas in the larger types it is a rounded and elaborately crenated rim. The functional significance of this conspicuous internal cingulum is not clear, and there is no special feature in the lower molars from which it might be possible to infer its existence in the upper molars. The presence of an internal cingulum is certainly a primitive feature of the upper molars and in this respect *Proconsul* is primitive. On the other hand, its marked tendency to elaboration is more reasonably regarded as a specialization characteristic of this genus. Among other characters of the upper dentition of *Proconsul* are, the relatively small size of the incisors in comparison with those of the modern Ponginae; the powerful development of the canines in the larger species; the downward prolongation of the sharply pointed buccal cusp of P$\underline{3}$ (particularly in the smaller species); the sharply circumscribed trigon which is somewhat constricted in proportion to the occlusal surface as a whole; the relatively large and well-defined hypocone, which is approximately equal in size to the cusps of the trigon in *P. africanus* but relatively smaller in *P. nyanzae*; the tendency in the larger species towards an enlargement of the protocone; the development at a forward angulation of the crest between the protocone and paracone of a protoconule which in *P. africanus* is hardly more than "incipient" but in the larger species forms a definite rounded tubercle; and the retrogressive tendencies of M $\underline{3}$ (particularly in *P. africanus*). In the lower dentition the main characters are the relatively small size of the incisors; the strongly developed and vertically implanted canines; the sectorial form of P $\overline{3}$; the well-developed hypoconulid in all the molars and the disposition of the main cusps in a "*Dryopithecus* pattern"; the remarkably small size of M $\overline{1}$; the persistent traces of an external cingulum, particularly in M $\overline{3}$; the rectangular contour of the occlusal surface in M $\overline{1}$ and M $\overline{2}$; and the elongated and tapering talonid portion of M $\overline{3}$.

A comparison of *Proconsul* with the great variety of Dryopithecinae found in other parts of the world, mostly from Upper Miocene and Lower Pliocene deposits, is not easily made. There has undoubtedly been a tendency in the past to multiply species and genera unnecessarily, and some of the forms which have been defined have been based on single teeth. Thus, it is a matter of some difficulty to sort out the types in order to test the validity of the criteria on which specific and generic distinctions have been made. The comprehensive work of Gregory & Hellman on the dentition of *Dryopithecus* (1926) gives a somewhat confused picture of their relationships; the same is true of Pilgrim's studies of hominoid remains from the Siwalik formations (1915, 1927), and of the report by Gregory, Hellman & Lewis (1938) on the fossil anthropoid apes collected by the Yale-Cambridge India Expedition. The vagueness of some of the diagnostic criteria is made particularly apparent in the systematic account of the Siwalik mammals given by Colbert (1935) who, in his treatment of the Hominoidea, has had to rely on the work of a number of previous authors. In 1937, Lewis made a bold attempt to simplify the taxonomy of the Siwalik fossils, in the course of which he eliminated the genus *Dryopithecus* from the Indian fauna, and included all those specimens attributed by Pilgrim to *Dryopithecus* in the genus *Sivapithecus*. Probably, however, he was influenced too much by geographical considerations, and thus tended to over-simplify the classification. For example, so far as the upper dentition is concerned, the molars of *D. punjabicus* Pilgrim show a number of features which contrast rather strongly with *S. sivalensis* (Lyddeker), but conform much more closely with the upper molars found in Europe and previously assigned to *Dryopithecus* (see p. 64 for a discussion on the contrasting features of the upper molars of *Dryopithecus* and *Sivapithecus*). Lewis would even transfer some of the *Dryopithecus* remains found in Europe to the genus *Sivapithecus* (e.g. certain molar teeth identified by Abel as those of *D. darwini*), but there seems no sound reason for such a conclusion.

So far as the size of the teeth is concerned, the different species of *Proconsul* can be paralleled by dryopithecine remains found elsewhere. The small third molar of *D. brancoi* * (=*Neopithecus brancoi* of Schlosser) closely resembles in its dimensions and appearance that of *P. africanus* (particularly specimen C.M.H.102), though in the latter the talonid is more complicated by secondary cuspules. The second and third molars of *P. nyanzae* approximate in size to those of *D. fontani*. The large molars of *P. major* correspond in size to the isolated third molar of *D. giganteus* from the Lower Pliocene of the Siwalik formations (and also, in some degree, to *Sivapithecus indicus*). All these species of *Dryopithecus*, however, are considerably later than *Proconsul*.

The general similarity between the mandibular teeth of *Proconsul* and those of *Dryopithecus* and *Sivapithecus* is very striking, but in several features they show significant differences. Perhaps the most conspicuous of these is the relatively small size of the first molar in *Proconsul*. A small first molar is rather characteristic of *Dryopithecus* and also of some of the Cercopithecidae (Smith Woodward, 1914), but its reduction has evidently proceeded further in *Proconsul*. In nine specimens of the genus *Proconsul*, the M $\overline{1}$/M $\overline{2}$ ratio ranges from 73 per cent. to 89 per cent., with a mean value of 80·9 per cent., and in only one case (*P. africanus*, S.21) exceeds 83 per cent. In eight specimens of *Dryopithecus* and *Sivapithecus* the ratio ranges from 83 per cent. to 93 per cent., with a mean value of 88·6 per cent., and in only one case reaches as low as 83 per cent. The presence of an external cingulum in *Proconsul* is another characteristic feature. This structure, however, is also present in the lower molars of *D. fontani*, though apparently not so strongly developed, and it has also been figured and described in a third molar of *D. darwini* by Abel (1902). Lastly, the tendency for the inner margin of the last molar to become broken up into irregular secondary cuspules in *Proconsul* distinguishes it from the more simply constructed tooth in most of the European and Asiatic Dryopithecinae. While the retention of an external cingulum in *Proconsul* is undoubtedly a primitive feature, the reduction in size of M $\overline{1}$, and the elaboration of the inner margin of M $\overline{3}$, are probably to be regarded as secondary specializations.

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* This tooth was at first assumed by Branco (1898) to be a second deciduous molar, but according to Schlosser (1901) its identification as a third permanent molar seems reasonably certain.

As already mentioned, the upper molars of *Proconsul* are much more distinctive than the lower molars; indeed the upper molars generally are more useful than the lower for differentiating one dryopithecine type from another. Unfortunately, however, the upper molars of *Dryopithecus* and *Sivapithecus* available for study are few in number. So far as we are aware, only five upper molars of *Dryopithecus* from Europe are certainly known—a first molar of *D. darwini* described by Glaessner (1931), two upper molars (one unerupted and one much worn) of *D. rhenanus* (=*germanicus*) described by Branco (1898), a third molar of *D. fontani* described by Depéret (1911), and an upper molar (? deciduous) of *D. darwini* (=*Griphopithecus suessi*) described by Abel (1902). All these specimens contrast strongly with *Proconsul* in the absence of an internal cingulum (except possibly for vestigial traces, as evident, for example, in one of Branco's specimens), in the larger trigon resulting from a splaying apart of the main cusps, and in the relatively large size of the paracone. The same contrasts are found in the upper molars of *D. punjabicus* Pilgrim. In *Sivapithecus* the trigon is more constricted, but the simplicity of the cusp pattern and the absence of a pronounced internal cingulum are again distinguishing features in which this genus differs widely from *Proconsul*.

In the general proportions of the horizontal ramus of the mandible, there is broad agreement between *P. nyanzae* and *D. fontani*, but the symphysial region shows certain significant differences. In *P. nyanzae* it may reach much more massive proportions (see text-fig. 11), possibly a sexual character associated with the large roots of the canine teeth, and there is no indication of a simian shelf. In *Dryopithecus fontani* there appears to be an incipient simian shelf (as indicated in the illustrations given by Smith Woodward, 1914). On the other hand, Gregory & Hellman (1926) figure a section through the symphysis of *D. pilgrimi* in which the shelf is clearly undeveloped; but there is some doubt about the generic identity of their specimen, which Lewis (1937) identified as *Sivapithecus sivalensis*. Lastly, the median axis of the symphysis in *P. nyanzae* is more vertical. This is clearly shown in MacInnes' figure (1943) of a section through the symphysis of the 1942 mandible, and also in the specimen S.28, 1947 which we have described (see text-fig. 11), where the symphysial axis is disposed at an angle of approximately 70° (cf. the angle of 54° given by Brown, Gregory & Hellman, 1924, for *D. pilgrimi*). The verticality of the symphysis in *Proconsul* is perhaps to be regarded as a primitive rather than an advanced character; it is paralleled in the modern *Symphalangus syndactylus*, in which Schultz (1933) notes that the chin is less receding than in any other primate except man. In *P. major* the angle of the symphysis is similar to that of *P. nyanzae*, i.e. about 70°, but in the smaller *P. africanus* it is more sloping.

The only other parts of the skeleton by which it is possible to compare *Proconsul* with *Dryopithecus* are the limb bones. Here, however, comparisons must necessarily be very tentative because of the paucity and uncertainty of the material. Besides the shaft of the humerus of *D. fontani* known from the material described by Lartet in 1856, the only other limb bone probably attributable to *Dryopithecus* is the femur described by Pohlig in 1895 as an unknown hominoid genus, *Paidopithex*, now generally assumed to belong to some form of *Dryopithecus* (see Schlosser, 1902). The humeral and femoral fragments described in this monograph are provisionally assigned to *Proconsul* only because their dimensions appear to conform with those which might be expected of the limb bones of that genus. There is a remarkable similarity in size and proportions between the humerus and femur of *Proconsul* and those of *Dryopithecus*. In the latter, the femur shows slight differences of detail in the upper extremity (particularly in the morphology of the lesser trochanter) and perhaps approaches the modern anthropoid apes a little more closely in this respect. Unfortunately the lower extremity of the femur attributed to *Proconsul* is missing, for this would have provided an important point for comparison with *Dryopithecus*, and no doubt would also have yielded useful information regarding posture and gait.

The relationships between *Proconsul* and the Dryopithecinae of Europe and Asia are not easy to assess. So far as the lower dentition is concerned, *D. fontani* appears to approximate most closely to *P. nyanzae* in the dimensions of its teeth and in the persistence of traces of the external cingulum on the molars. But, as we have seen, the few upper molars available of *Dryopithecus* indicate that they differ in several respects. Of the Siwalik genera, *Ramapithecus* and *Sugrivapithecus* appear to be rather widely divergent forms with relatively small teeth and delicately constructed jaws, and with canines of remarkably small size. In *Sugrivapithecus*, also, the molars are conspicuously narrow. *Bramapithecus* offers a more favourable comparison, particularly in the presence of a reduced external cingulum in the lower molars, and in the form of the last molar, in which the lingual border of the crown tends to break up into secondary cuspules as in *P. nyanzae* (Gregory, Hellman & Lewis, 1938). However, the remains of this genus are too scanty to permit definite conclusions.

Sivapithecus has a relatively simple molar structure, particularly in the maxillary teeth. So far as this genus is concerned, however, comparison with *Proconsul* is perhaps of secondary importance, for there existed another type of large hominoid in the Miocene period of East Africa, contemporaneous with *Proconsul*, which, on the basis of the upper dentition, appears to be indistinguishable from *Sivapithecus*. This species, *S. africanus*, is probably of much earlier date than the Indian species and may well bear an ancestral relationship to them. However, the remains of *S. africanus* so far obtained in Kenya are very few and fragmentary, and we must wait for further accessions of material before its systematic position can be more certainly defined.

Whether *Proconsul* can be regarded as having any ancestral relationship to the European forms of *Dryopithecus* depends largely on the interpretation of its apparent specializations—particularly the strong and elaborate development of the internal cingulum in the upper molars. It is possible, of course, that, by the gradual reduction and eventual disappearance of the internal cingulum, upper molars of the *Dryopithecus* type might have been derived from those of the *Proconsul* type. While such a possibility can hardly be denied, it seems more likely that the tendency towards the elaboration of the cingulum in *Proconsul* is a local specialization of a slightly aberrant type. Such an interpretation would render somewhat less probable the view that this genus could have given origin to *Dryopithecus*.*

The contrast between *Proconsul* and the Dryopithecinae of Europe and Asia raises the question whether the former should be allocated to a separate subfamily of the Pongidae. However, apart altogether from considerations of taxonomic convenience, the resemblances in the morphological details of the lower dentition appear to us to make such a distinction undesirable, at least for the present.

Between the primitive *Propliopithecus* of Oligocene times, and the remarkable assemblage of large anthropoid apes which appeared in the early Miocene of East Africa, there seems to be a considerable morphological hiatus. In this connection, the question of the origin of *Proconsul* naturally presents itself. Presumably it was derived from some advanced hylobatine type similar to *Limnopithecus*. In fact, the gap separating the small *P. africanus* from *Limnopithecus* is not perhaps so marked as might appear to be the case on superficial consideration. For example, the upper molars of *L. macinnesi* show a well-developed internal cingulum which already appears to be slightly complicated by a fine beading and thus to adumbrate the characteristic appearance of the upper molars of *P. africanus*. A transformation of the type envisaged would involve, among other things, a progressive increase in body size, a relative deepening of the mandible, an increase in the size of the canines with a concomitant thickening of the symphysial region, a conversion of the shape of the molar cusps from a rounded tubercular form to a relatively broader and more pyramidal form, and a relative reduction of the first lower molar. The anterior lower premolar of *L. macinnesi* was probably too specialized by its lateral compression to provide an antecedent for the corresponding tooth in *Proconsul*, and the upper canines were perhaps too elongated and sabre-like, but these specializations are not present in *L. legetet*. It may be suggested that *Propliopithecus* gave rise to a more advanced hylobatine ape of the *Limnopithecus* type which provided the basis for the evolutionary development of *Proconsul*, and that the species of *Limnopithecus* which existed contemporaneously with *Proconsul* represent survivals, not greatly modified, of this ancestral stock.

We have now to consider the relationship of *Proconsul* to the modern representatives of the Hominoidea. Hopwood (1933*a*) called attention to the primitive features of the dentition of *Proconsul* and at the same time noted certain resemblances to the chimpanzee. For example, he stated that there appears to be no definite criterion by which $P\overline{3}$ of the fossil genus can be distinguished from that of the chimpanzee. On the other hand, *Proconsul* (as with the Dryopithecinae in general) agrees more closely with the gorilla in the sharp definition of the main cusps of the molar teeth, the development and disposition of the hypoconulid, and the relatively smaller entoconid. Further, the progressive increase in length of the lower molars from first to third is sometimes found in the gorilla. Traces of the external cingulum are also to be found quite often on the lower molars of the gorilla, but only exceptionally in the chimpanzee. In its general features, there appears no sound reason against the suggestion that the *Proconsul* group provided the ancestral stock from which the modern African anthropoid apes were derived in the course of evolution but, as in our consideration of possible relationships with the Dryopithecinae, account must be taken of the significance of the apparent specializations in the molar teeth of *Proconsul*, particularly the strong development of the internal cingulum. However, vestiges of an internal cingulum are not uncommonly found in the upper molars of the chimpanzee, and in some cases these traces may even show a faint crenation. Possibly therefore, in later phases of evolution, the pronounced cingulum of *Proconsul* may have undergone retrogressive changes so as to lead to a type of molar characteristic of the modern chimpanzee. The varied population of primitive anthropoid apes in East Africa in early Miocene times, taken in conjunction with the earlier and more primitive forms from the Oligocene of Egypt, *Parapithecus* and *Propliopithecus*, certainly enhances the probability that the whole group of anthropoid apes (including both the Hylobatinae and Ponginae) originated somewhere on the African continent. However, the upper and lower molars of *Pondaungia* and the mandibular fragment of *Amphipithecus*, both from the Upper Eocene of Burma, clearly call for some caution in making a definite statement on this problem until further evidence becomes available.

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* The possibility that representatives of the genus *Proconsul* may have persisted in East Africa to a much later date is raised by Lönnberg's discovery of two upper canines and two upper premolars of a large ape (which he called *Proconsuloides naivashae*) in Gamblian deposits south-east of Lake Naivasha. However, this material is too scanty for a conclusive comparative study.

Apart from the question of special relationships between *Proconsul* and other genera of recent or extinct anthropoid apes elsewhere, the remains of this early Miocene form provide most important evidence of a general nature regarding the evolution of the Hominoidea. For if they may be accepted as a representative sample illustrating the stage of evolution reached by the Hominoidea in early Miocene times, they are clearly pertinent to the problem of the evolutionary origin of the whole group of anthropoid apes, and also of man himself.

From the evidence which we have presented, it is apparent that the early Miocene apes were in many respects exceedingly primitive. So far as can be inferred from the skull of *P. africanus*, the brain had advanced but little beyond the cercopithecoid stage, with relatively small frontal lobes showing a simple convolutional pattern, and with a cerebellum in which the lateral lobes had not yet expanded to the proportions found in the modern large apes.*

In the morphology of the skull, *Proconsul* also shows a number of primitive characters in which it approximates at the same time more closely to the smaller cercopithecoid monkeys than to the modern large apes. These characters include the shape of the nasal aperture (which narrows at its lower extremity), the abbreviated sub-nasal part of the premaxillary region, the orientation of the orbital apertures, the absence of a pronounced post-orbital constriction of the skull, the narrowness of the symphysial region of the mandible, and the lack of a simian shelf. The lightness of construction of the skull in *P. africanus*, with the complete absence of even an incipient supra-orbital torus, and the delicate build of the zygomatic region, is again in contrast with the modern large apes, though it remains possible that in the larger species of *Proconsul* the skull may have developed more rugged features.

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* So far as the available evidence goes, the stage of evolution represented by the brain of these extinct apes appears to have been approximately parallel to that shown in some other mammalian groups. For example, Edinger (1948) has shown that in the early Miocene representative of the Equidae, *Parahippus*, the brain was small with relatively poorly developed frontal lobes and, although the main sulci were already evident, the more complicated pattern of secondary sulci had not yet appeared.

The skull of *P. africanus* appears rather markedly prognathous in comparison with the modern apes, but this is partly illusory because of the absence of a strongly projecting supra-orbital torus (which, of course, advances quite considerably the glabella and nasion beyond the frontal pole of the brain-case). On the other hand, the proportions of the mandible in *P. nyanzae*, as well as the evidence provided by the maxilla in specimen C.M.H.2, indicates that in this larger species the contour of the facial part of the skull in lateral view must have approached much more to the vertical.

It seems reasonable to infer from the evidence of the Miocene fossils that the characteristic features of the skulls of the African apes of to-day, such as the powerful supra-orbital torus, the large circular and forwardly directed orbits associated with a strong development of their lateral margins, the broadening of the lower extremity of the nasal aperture, the extension downwards and forwards of the sub-nasal part of the premaxilla, the widening of the symphysial region of the mandible in association with a relative hypertrophy of the incisor teeth, and the development of a simian shelf, were probably all secondary developments which appeared at a later stage of evolution.*

The limb bones identified as those of *Proconsul* (probably *P. nyanzae*) are of particular interest for the reason that, in discussions on the relationships of the modern anthropoid apes and their evolutionary history, much argument has been expended in the past on the significance of the adaptive specializations for an arboreal mode of life which they show in their limb structure. It now appears that the limbs of the early Miocene apes were very different from those of the recent Pongidae. The straightness and slenderness of the shafts of the humerus and femur indicate relatively lightly built and agile creatures. More important, however, are the details of the upper extremity of the femur, the forward curvature of the middle of the humeral shaft, and the proportions and detailed morphology of the talus and calcaneum, which, taken in combination, conform with a cercopithecoid type of limb skeleton associated with quadrupedal locomotion, and at the same time provide no evidence that a brachiating mode of life had been adopted. The early Miocene apes of East Africa, it appears, were active, running and leaping creatures and in no way specialized for a purely arboreal habitat.† It will be observed that the evidence of limb morphology is consistent with that of the brain. For if it may be assumed that the elaboration of the frontal lobes and the cerebellar hemispheres in the modern Hominoidea has some relation to the complicated patterns of muscular co-ordination needed for balancing in the erect position, then their relatively poor development in *P. africanus* would seem to preclude such a posture in this fossil ape, at least as an habitual activity. On the other hand, we have noted certain features in the calcaneum—the strong development and posterior position of the basal tubercle and the backward extension of the main talar facet—which may have permitted a greater component of the weight of the body to be thrown backwards towards the heel than in the modern apes if the creature attempted momentarily to rear up on its hind limbs.

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* In the absence of a strong supra-orbital torus the orang clearly preserves a primitive feature in which it resembles *Proconsul* more closely than do the African apes, though, in fact, the morphology of the orbital region in this Asiatic ape is very different in other details from that of *P. africanus*.

† Schlosser (1901) suggests, on the evidence of the Eppelsheim femur, that the European *Dryopithecus* of lower Pliocene date may have still been largely quadrupedal in its activities.

No doubt we must await the discovery of more limb material of these early apes before coming to a definite conclusion on their mode of locomotion. But the type of hind limb which they evidently possessed provides a suitable antecedent for the subsequent evolutionary development along divergent lines of the brachiating specializations of the modern large apes on the one hand, and of the type of limb structure required for the erect posture characteristic of the Hominidae on the other. Thus, although the early Miocene apes may have no immediate reference to the emergence of man, their importance in connection with this problem is obvious. There is a general consensus of opinion that the Hominidae and the Pongidae separated in their evolutionary divergence from a common ancestral stock probably in the Miocene, or possibly earlier, and even if the early Miocene apes of East Africa themselves do not include representatives of this ancestral stock, presumably, because of their great antiquity, they approximate rather closely to it in at least some of their anatomical features.

In spite of these rich East African discoveries, our knowledge of the early fossil Hominoidea still remains very incomplete. Nevertheless, it is permissible to consider the bearing of this new material on hypotheses regarding the evolution of the Hominoidea as a whole. Any such hypothesis will, of course, have to be tested, and if necessary revised, with each new accession of palaeontological evidence. However, the following brief statement of hominoid evolution appears to accord with the facts available at present. The earliest forms which can be seriously considered as "anthropoid apes" on the basis of tooth structure are *Parapithecus* and *Propliopithecus* of Oligocene date. From the latter probably arose hylobatine types referable to the genus *Limnopithecus*, which by the early Miocene had split up into at least two species: the larger, *L. macinnesi*, became markedly specialized in the development of long canines and compressed lower premolars; the smaller and relatively unspecialized *L. legetet* may have given rise to *Pliopithecus*, and ultimately to the modern Hylobatinae. Another type of anthropoid ape appeared at the very beginning of the Miocene period, probably also derived initially from a generalized *Limnopithecus* stock. This was an early representative of the genus *Proconsul*, which was no doubt quite a small and lightly built creature. From this, again, arose a rather rapid series of evolutionary radiations of diverse types and of different sizes. Thus, in the early Miocene, larger apes of the size of the modern chimpanzee and gorilla had already come into existence. These types showed minor specializations of the dentition which may have excluded them from any direct ancestral relationship to the Dryopithecinae of later date. However, contemporaneously with *Proconsul* there appears also to have existed a type of large ape (*Sivapithecus africanus*) in which these dental specializations were not present. It seems probable that this species (of which, unfortunately, very few remains have so far been found) had a common origin with *Proconsul*, and it may have provided the ancestral stock from which the European and Asiatic Dryopithecinae were derived. Certainly it had very close affinities with the Indian species of *Sivapithecus*. The Hominidae diverged from the Pongidae, it is suggested, perhaps in the Miocene, when the early anthropoid apes still possessed a limb structure similar to that of *Proconsul*. From an ancestral group with limbs of this type, the modern anthropoid apes developed their characteristic brachiating specializations, and from a consideration of geographical factors and migrational difficulties, these perhaps developed in the gibbon and orang independently of the chimpanzee and gorilla. In another direction, the precursors of the Hominidae arose, probably without passing through a brachiating phase, by the gradual conversion of limbs of the *Proconsul* type into limbs adapted for upright progression. The details of such a transformation are, of course, quite conjectural, and must remain so until we have some knowledge of the limb structure of the later Miocene and early Pliocene fossil hominoids. But such a conception of the origin of the Hominidae would obviate the difficulties expressed by many comparative anatomists in supposing that limbs of the human type could have been derived by a type of retrograde evolution from the highly specialized limbs characteristic of the modern large apes (see Morton, 1924).

In conclusion, it seems desirable to make some reference to the application of the term "anthropoid ape" to early Miocene types such as *Proconsul*. In a number of anatomical features, *Proconsul* resembles the Cercopithecoidea, and the question may be raised whether it is in fact proper to include the genus in the Hominoidea. However, as the palaeontological evidence of evolutionary sequences accrues, definitions may from time to time require to be broadened so as to include the earlier as well as the recent representatives of any single natural group. The evidence so far available indicates clearly that the Cercopithecoidea diverged from the Hominoidea at least in Oligocene times. *Moeripithecus* and *Apidium* may be taken to represent the early phases in this evolutionary segregation, and the remains of *Mesopithecus* from East Africa show quite definitely that the Cercopithecoidea had already by the early Miocene achieved their characteristic dental specializations. On the other hand, it was to be anticipated that in the early phases of their evolutionary independence, the Hominoidea would still show many primitive features which, in modern primates, are distinctive of the Cercopithecoidea rather than the Hominoidea. This is undoubtedly the case with *Proconsul*, but in its dentition, particularly in the molar pattern which shows, among other things, a characteristic development of the hypoconulid, and in the proportions of the facial skeleton of the larger species as indicated by the mandible of *P. nyanzae*, this genus must certainly be regarded as an anthropoid ape, albeit of a very primitive type.

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BRITISH MUSEUM NATURAL HISTORY
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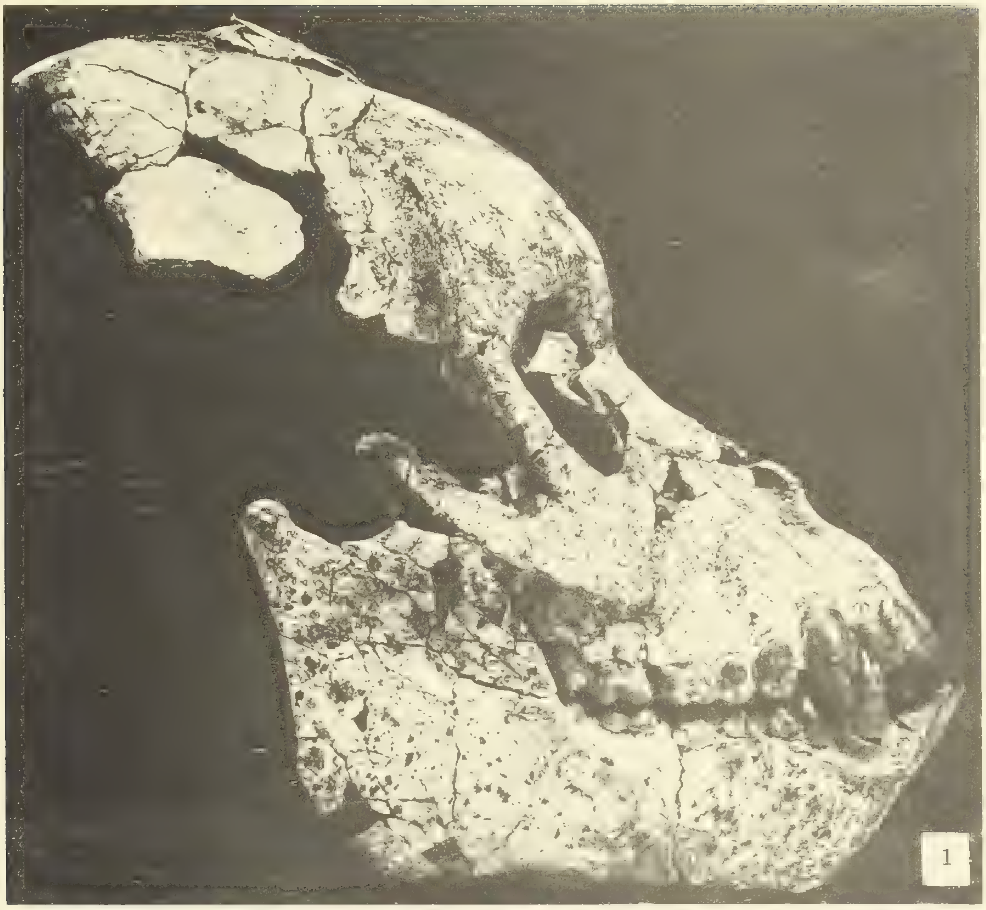
EXPLANATION OF PLATE I

Proconsul africanus. Specimen R.1948, 50

FIG. 1. Lateral view of skull. Natural size.
,, 2. Facial aspect of skull. Natural size.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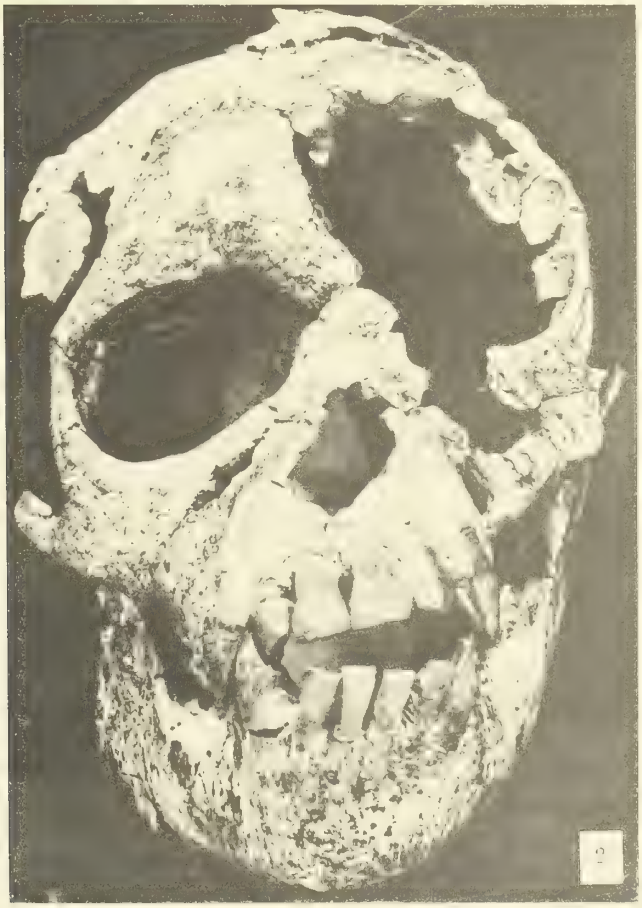
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PROCONSUL

PLATE II

EXPLANATION OF PLATE II

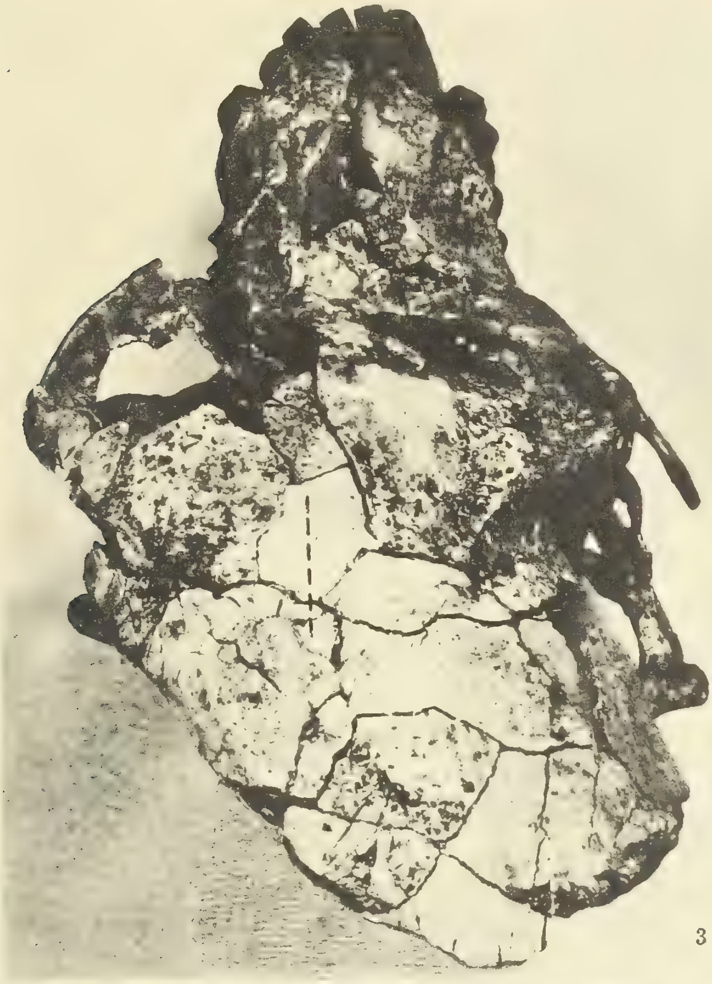
Proconsul africanus. Specimen R.1948, 50. *All natural size*

FIG. 3. Skull viewed from above. The interrupted line marks the mid-line of the cranial vault.

,, 4. Skull viewed from below.

,, 5. Mandible viewed from the occlusal aspect of the teeth.

,, 6. Mandible from the left side.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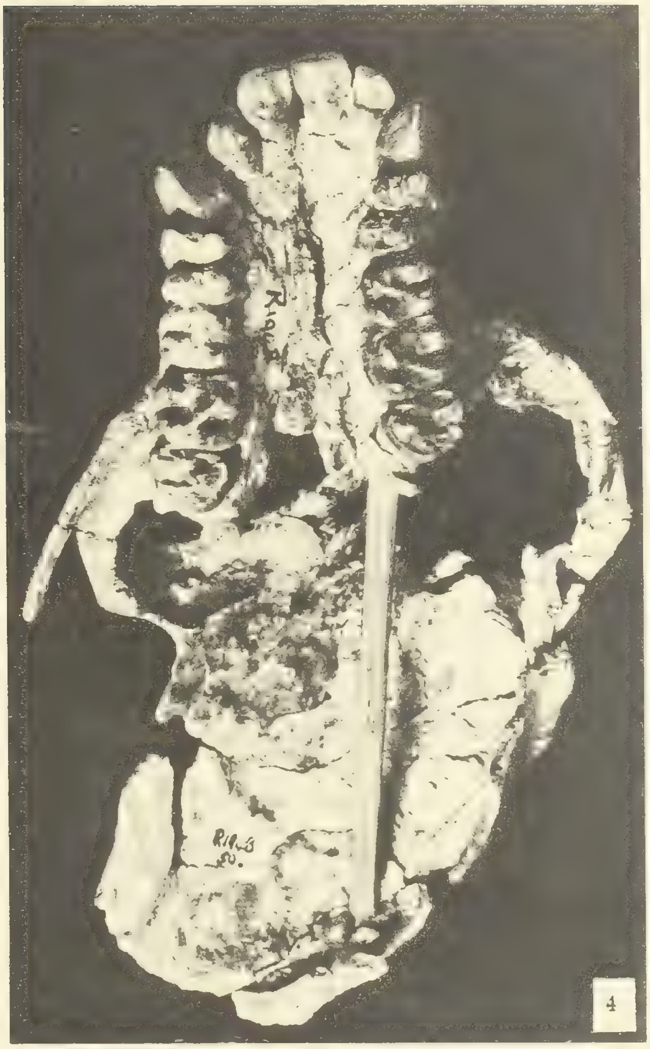
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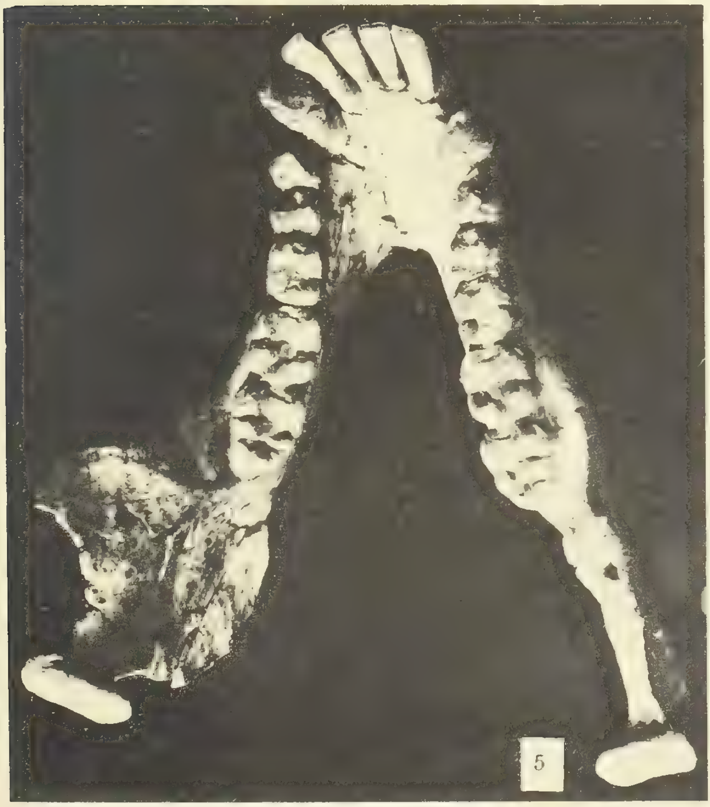
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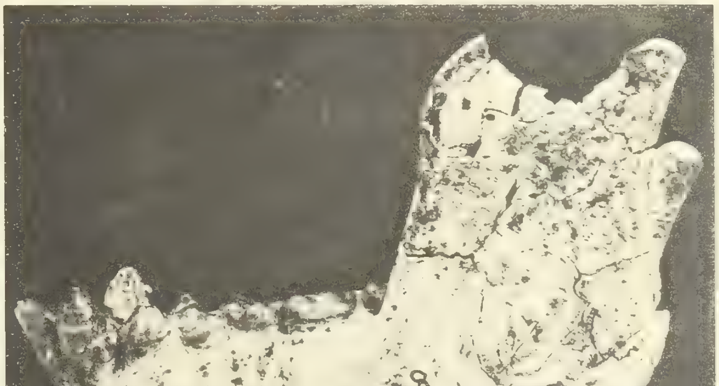
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PROCONSUL

PLATE III

EXPLANATION OF PLATE III

Proconsul africanus

FIG. 7. Occlusal aspect of the left maxillary teeth of holotype from Koru (M.14084). × 2. The teeth, which in the specimen are slightly dislocated from their natural position, are represented in their proper alignment.

,, 8. Mandible (C.M.H.102), viewed from the occlusal aspect of the teeth. Natural size. P$\overline{4}$–M$\overline{3}$ of the left side are in position, and the sockets for the two canines are seen.

,, 9. Mandible (C.M.H.102), viewed from the left side. Natural size. P$\overline{4}$–M$\overline{3}$ are in position, and in front is seen the socket for the canine and the stump of P$\overline{3}$. Behind the symphysial region the lower border of the mandible is deficient. The enamel on the lateral aspect of M$\overline{3}$ is partly broken away.

,, 10. Mandible (R.1948, 375), viewed from the occlusal aspect of the teeth. Natural size. The teeth are severely weathered, but the mandible itself is undistorted.

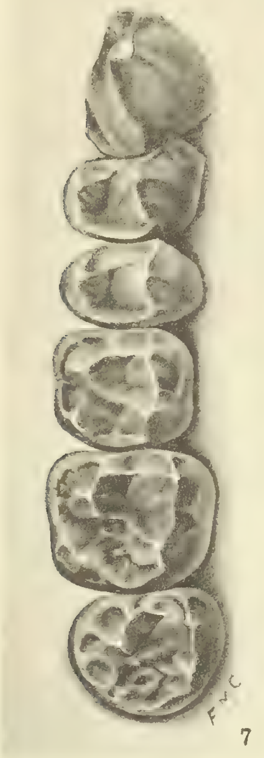
,, 11. Maxillary fragment of left side of ?*P. africanus* (S.15, 1947). × 2. P$\underline{4}$ and M$\underline{1}$ are in position.

,, 12. Left lower third molar. (1097). × 3.

,, 13. Left first upper molar of ?*P. africanus* (S.2, 1947). × 2.

,, 14. Right first upper molar of ?*P. africanus* (C.M.H.144). × 3.

,, 15. Left upper canine (C.M.H.103). × 1·9. Viewed from (a) the labial, and (b) the lingual aspect.



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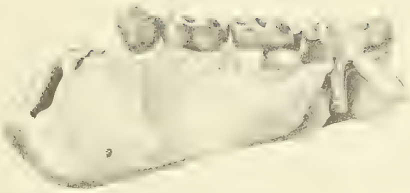

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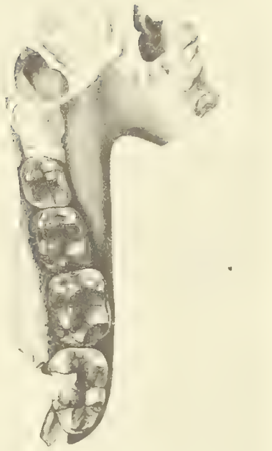

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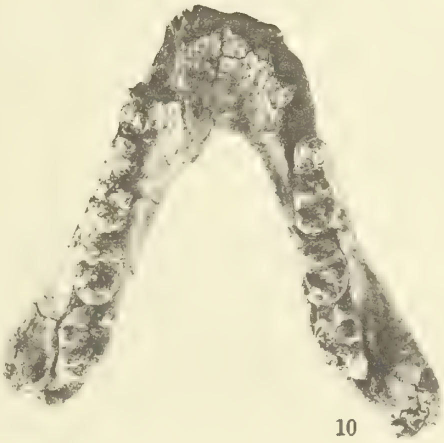

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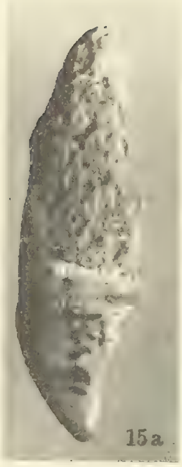

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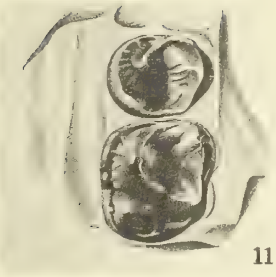

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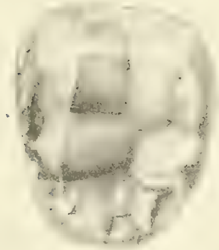

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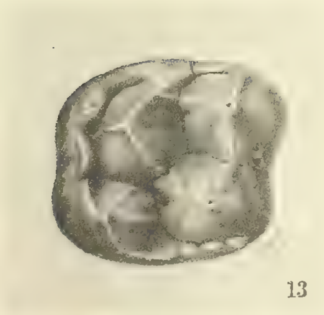

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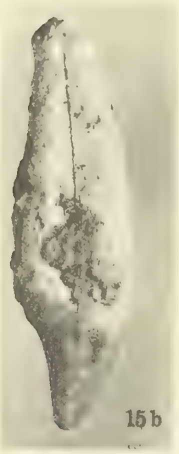

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PROCONSUL

PLATE IV

EXPLANATION OF PLATE IV

Proconsul nyanzae

FIG. 16. Occlusal aspect of left maxillary teeth (C.M.H.2). × 2. The last two molars, which are considerably displaced in the specimen, have been represented in their proper alignment.

,, 17. Occlusal aspect of right maxillary teeth (C.M.H.3). × 2. All the teeth show the effects of weathering. The last molar is in process of eruption.

,, 18. Right maxillary fragment (712, 1947), with the much worn premolar and molar teeth in position. × 2. This fragment belongs to the same individual as the 1942 mandible.

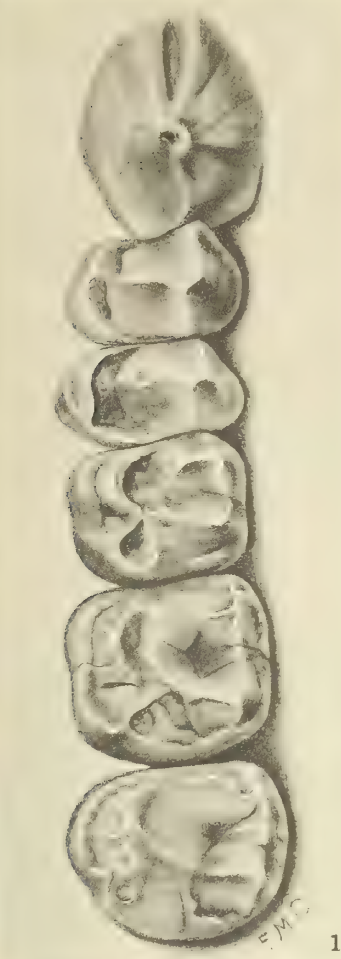
,, 19. Lower left premolar-molar series (C.M.H.4). Natural size. The teeth were found isolated and have been represented in approximate alignment. The relatively small size of the first molar should be noted.

,, 20. Left side of maxillary fragment (C.M.H.2). Natural size. The last two molars, which are considerably displaced in the specimen, have been represented in their proper alignment.

,, 21. Left side of the body of the mandible (S.28, 1947). Natural size. Only the stumps of the teeth remain in position.

,, 22. Immature mandible, viewed from the occlusal aspect of the teeth (C.M.H.110). × 1·2. The first molar has completed its eruption and is seen (broken anteriorly) on the left side. The posterior premolar and the second permanent molar are in process of eruption. In front are seen the stumps of the permanent incisors and the deciduous canine. This figure should be compared with the reconstruction of the mandible in text-fig. 13.

,, 23. Upper central incisors of ?*P. nyanzae*, viewed (a) from the labial, and (b) from the lingual aspect. On the left, in each pair, is a right central incisor (C.M.H.9), and on the right a left central incisor (C.M.H.10). × 1·9.



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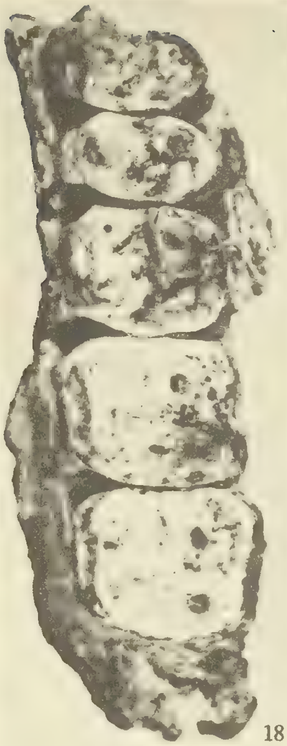

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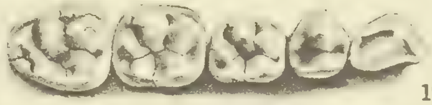

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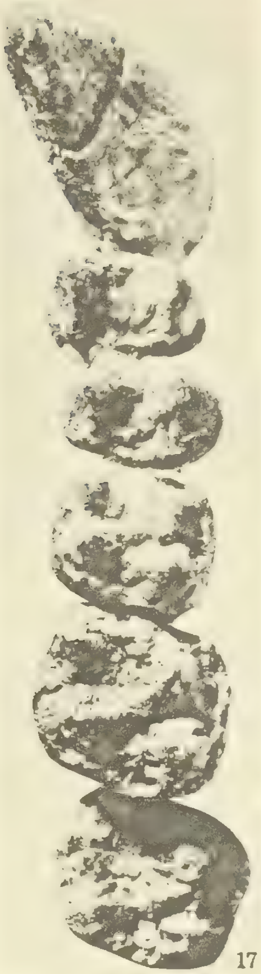

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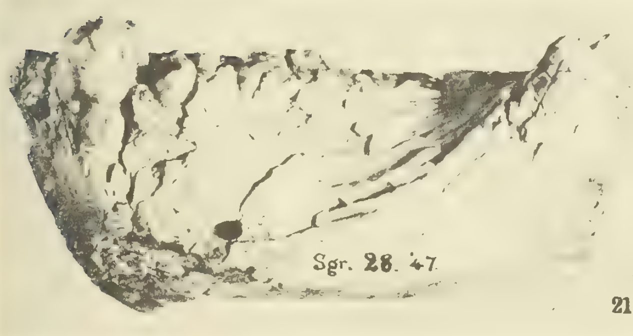

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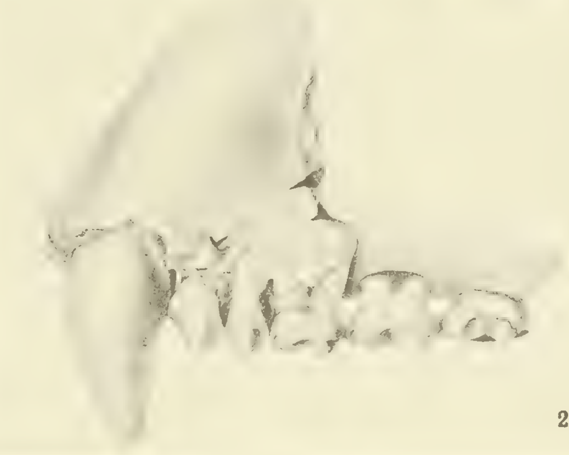

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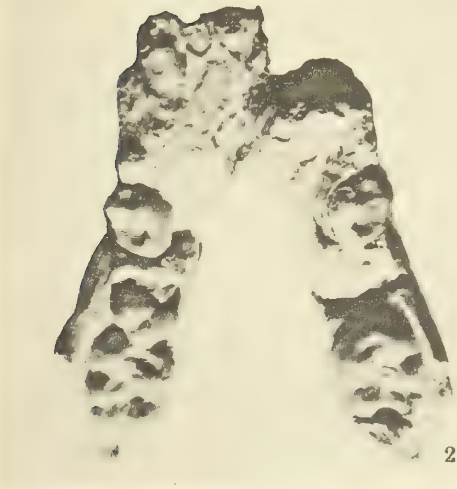

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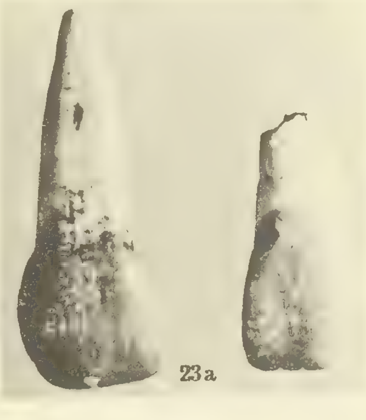

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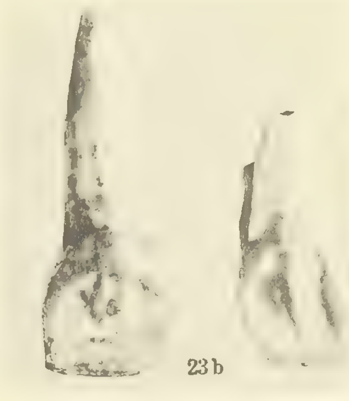


23b

PROCONSUL

PLATE V

EXPLANATION OF PLATE V

Figs. 24–33, Proconsul nyanzae

FIG. 24. Left upper second molar (933, 1947). × 3. This is an unerupted tooth which was embedded in the maxilla of an immature individual (see text-fig. 14a).

,, 25. Second right upper molar (C.M.H.122). × 3.

,, 26. First right upper molar (C.M.H.121). × 3. This specimen and that shown in the previous figure are unerupted teeth. In both cases the protoconule is distinct.

,, 27. Crown of unerupted third left upper molar (C.M.H.33). × 2·7.

,, 28. Second left upper molar (C.M.H.32). × 3.

,, 29. First right lower molar (683, 1947). × 2.

,, 30. Second right lower molar (C.M.H.135). × 2.

,, 31. Third right lower molar (143, 1947). × 2.

,, 32. Second left lower molar, partially erupted (C.M.H.110). × 2. This tooth is shown in position in Plate IV, fig. 22.

,, 33. Second right lower molar, unerupted. × 2·7.

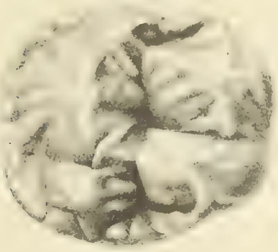
Figs. 34–37, Proconsul major. Natural size

,, 34. Fragment of the right side of the body of the mandible (S.80, 1947), viewed from the lateral aspect. The posterior premolar and the molars are in position, and all show a considerable amount of wear.

,, 35. The same specimen as that shown in the previous figure, viewed from the occlusal aspect of the teeth. The relatively small size of the first molar should be noted.

,, 36. Fragment of the symphysial region of the mandible (S.1, 1947), viewed from the right side.

,, 37. The same specimen as that shown in the previous figure, viewed from in front. The root of the left canine is seen exposed in its socket.



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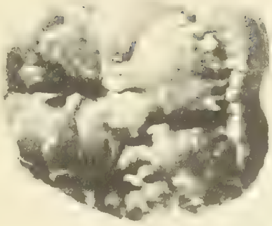

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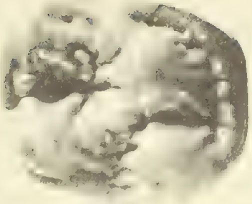

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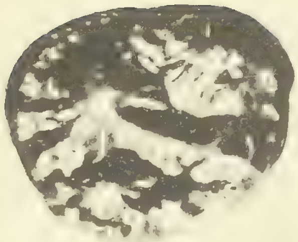

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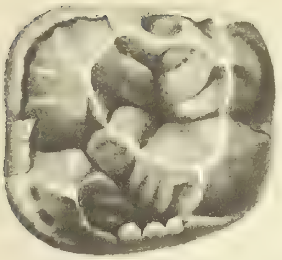

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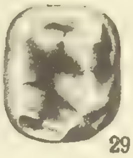

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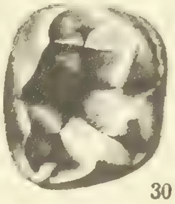

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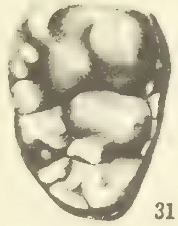

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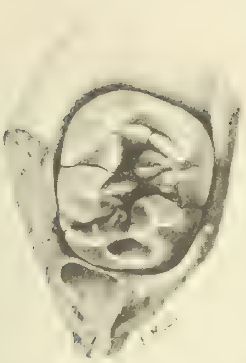

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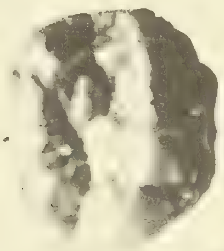

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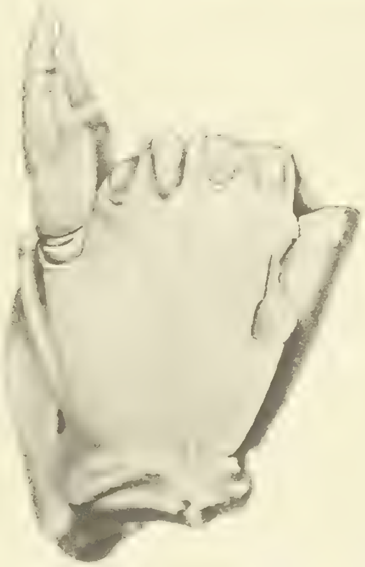

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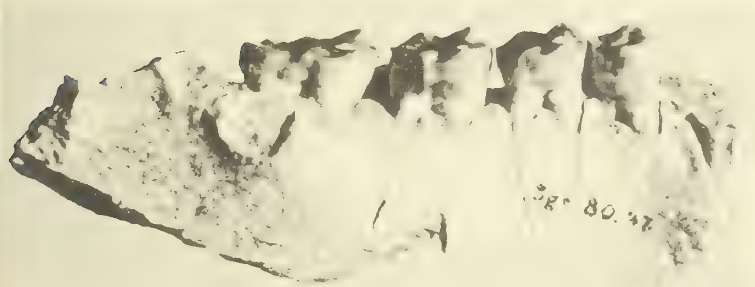

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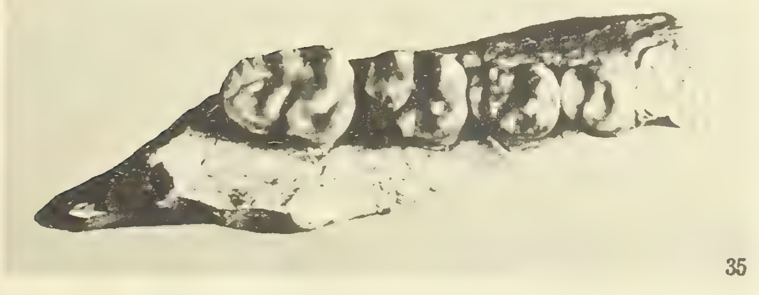

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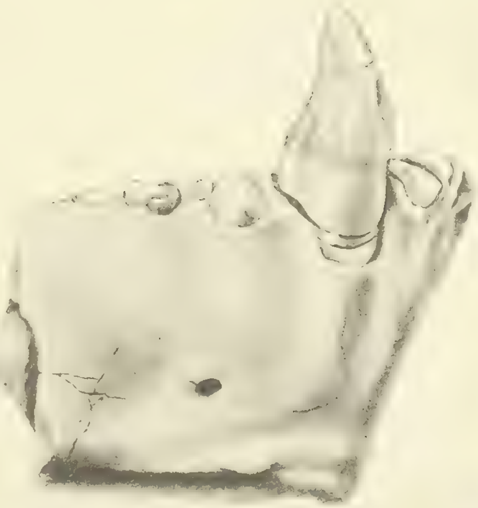

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PROCONSUL

PLATE VI

EXPLANATION OF PLATE VI

Figs. 38–40, *Proconsul major*

Fig. 38. Unerupted second left lower molar (S.55, 1948). × 2.

,, 39. Posterior left lower premolar (S.56, 1948). × 2.

,, 40. Second (?) right upper molar (C.M.H.35) provisionally attributed to *P. major*. × 1·7.

Figs. 41–45, *Sivapithecus africanus*

,, 41. Left maxillary fragment (C.M.H.6), viewed from the occlusal aspect of the teeth. × 2·1. The two premolars and the first molar are in position and, behind the latter, the stump of the second molar.

,, 42. The same specimen as that shown in the previous figure, viewed from the lateral aspect. × 2.

,, 43. First left upper molar from specimen C.M.H.6. × 3.

,, 44. Unerupted first right upper molar (C.M.H.26). × 3.

,, 45. Second right upper molar (C.M.H.27). × 2·7.

Figs. 46–51, *Limnopithecus legetet*

,, 46. Right mandibular fragment (S.13), viewed from the occlusal aspect of the teeth. × 2.

,, 47. Left mandibular fragment (C.M.H.106). × 2. The first and second molars are in position.

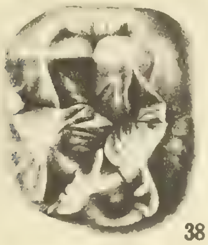
,, 48. Occlusal aspect of the teeth in a right maxillary fragment (S.120, 1948). × 2. The canine (with the tip broken off), the two premolars and the first molar are preserved. The first molar has been slightly displaced.

,, 49. First left lower molar (S.63, 1948). × 2.

,, 50. Second and third right lower molars (S.121, 1948). × 2.

,, 51. Left lower canine of ?*L. legetet* (C.M.H.20), viewed (a) from the labial, and (b) from the lingual aspect. × 1·9.

,, 52. Isolated canines provisionally attributed to *Limnopithecus*, viewed from (a) the buccal, and (b) the lingual aspect. The tooth on the left (S.7) is a left lower canine identified as *L. macinnesi*; the other two probably belong to *L. legetet*, a right upper canine in the middle (S.3, 1947), and a left lower canine to the right (S.17, 1947). All natural size.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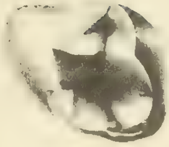
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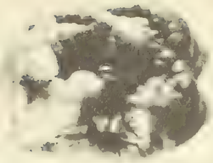
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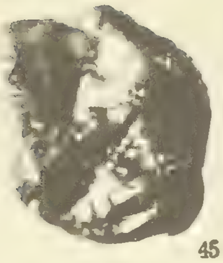
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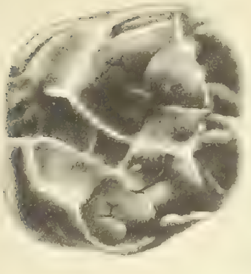
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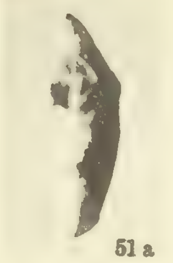
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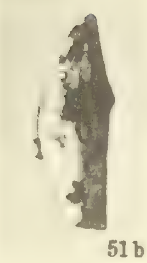
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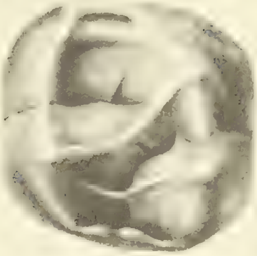
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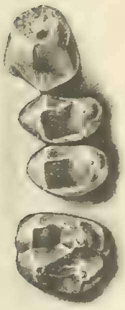
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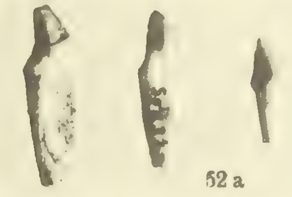
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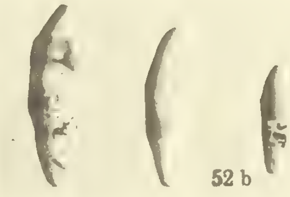
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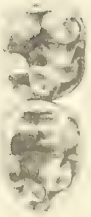
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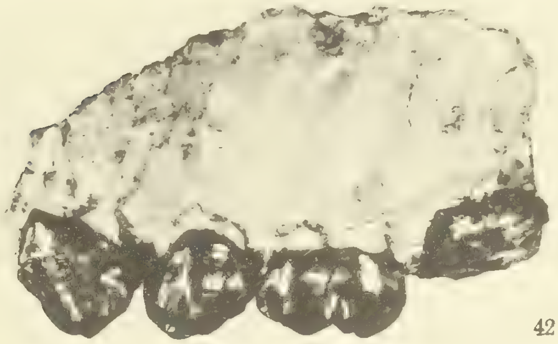
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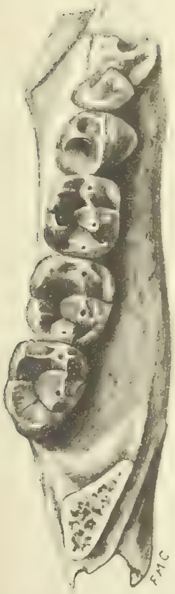

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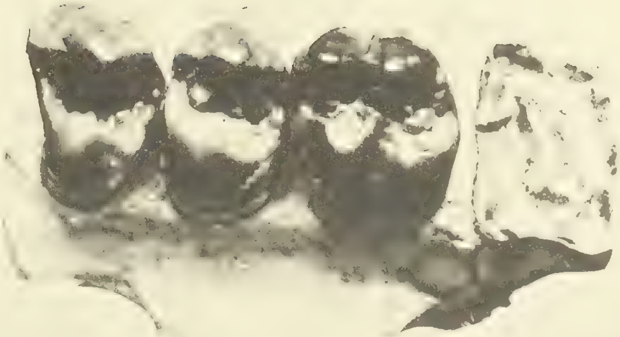
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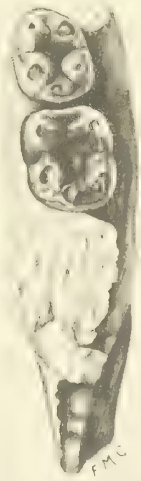

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PROCONSUL, SIVAPITHECUS, LIMNOPITHECUS

PLATE VII

EXPLANATION OF PLATE VII

Limnopithecus macinnesi

FIG. 53. Mandible (710, 1947). (a) Left half of body viewed from the lateral aspect. (b) Right half of body viewed from the medial aspect. × 1. On both sides the two premolars and the second and third molars are in position.

,, 54. Mandible (710, 1947), viewed from the occlusal aspect of the teeth. × 1·1. The two halves of the mandible have been placed in approximate relationship to each other as indicated by reference to the midline of the symphysial region.

,, 55. The lower teeth (the premolars and second and third molars) in the left side of the mandible (710, 1947). × 2.

,, 56. Symphysial fragment (S.29, 1947), viewed from in front. × 2. The right canine is in position, and the stumps of the two median incisors and the right lateral incisor.

,, 57. Left mandibular fragment (S.9, 1938), containing the two premolar teeth, viewed (a) from the lateral, and (b) from the medial aspect. × 2.

,, 58. Right maxillary teeth (545, 1947). × 2. The tip of the canine has been broken off.

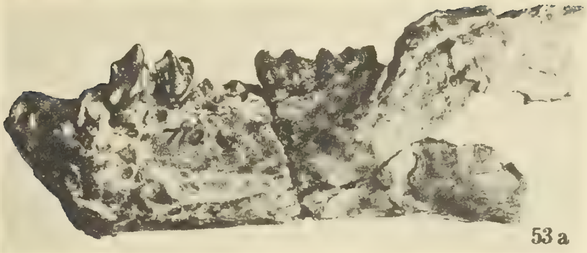
,, 59. Left maxillary fragment (S.57). × 2. The contour of the tip of the canine tooth has been restored.

,, 60. The same specimen as that shown in the previous figure, viewed from the palatal aspect. × 2.

,, 61. First right upper molar (667), probably unerupted. × 2. The slight beading of the internal cingulum should be noted.

,, 62. Upper left central incisor, much worn (S.H.), viewed (a) from the labial, and (b) from the lingual aspect. × 1·9.

,, 63. Left lower canine of ?*L. macinnesi* (S.7) viewed (a) from the labial, and (b) from the lingual aspect. × 1·9.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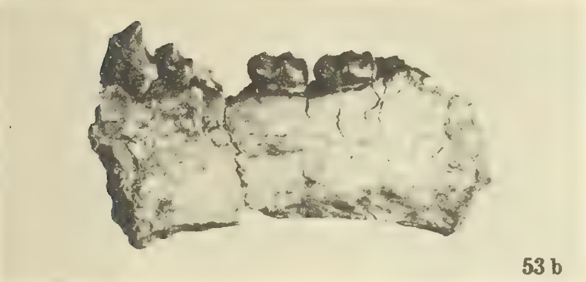
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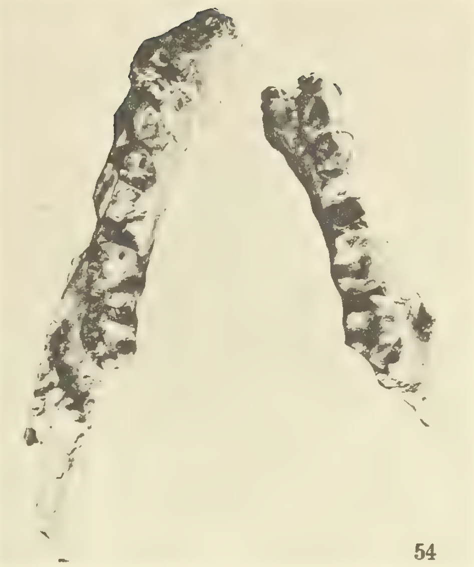
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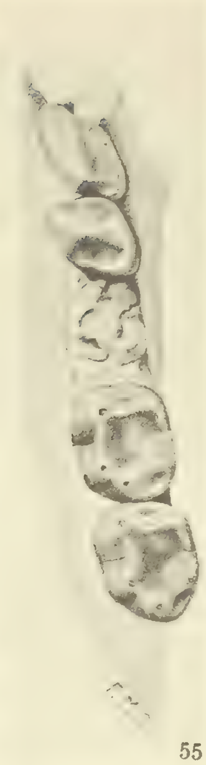
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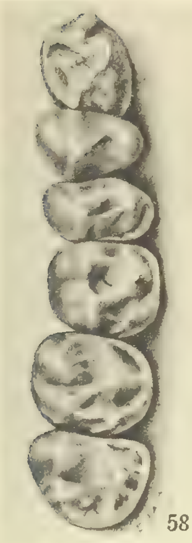
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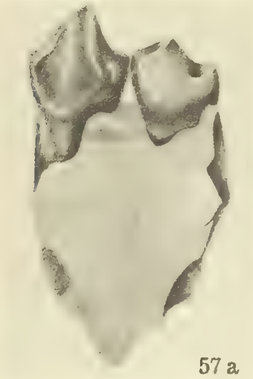
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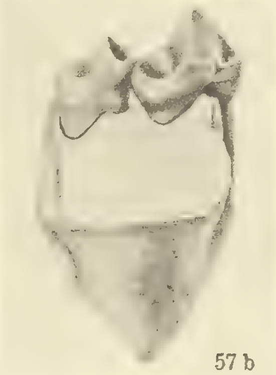
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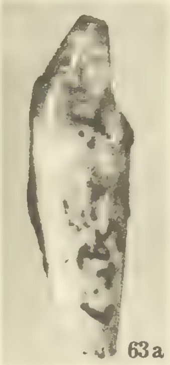
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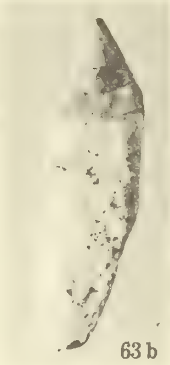
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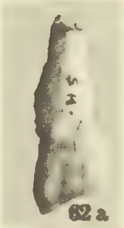
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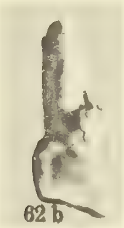
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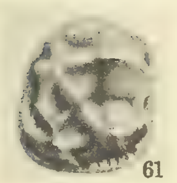
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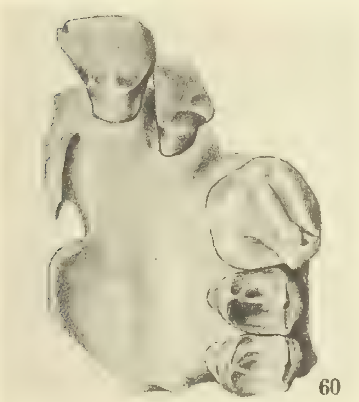
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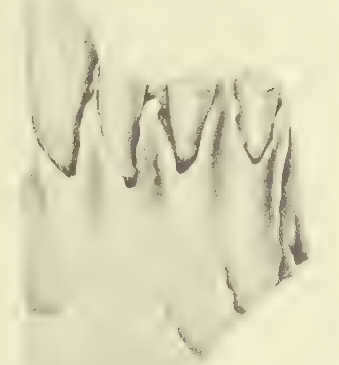
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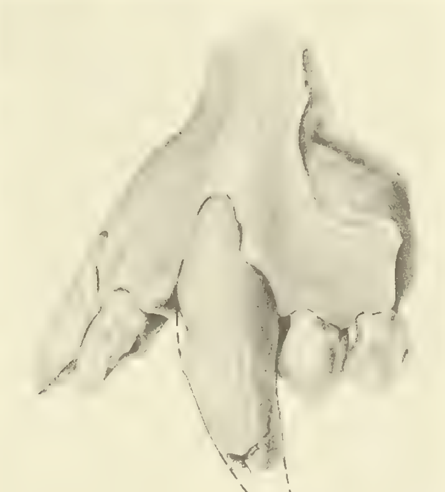

59

LIMNOPITHECUS

PLATE VIII

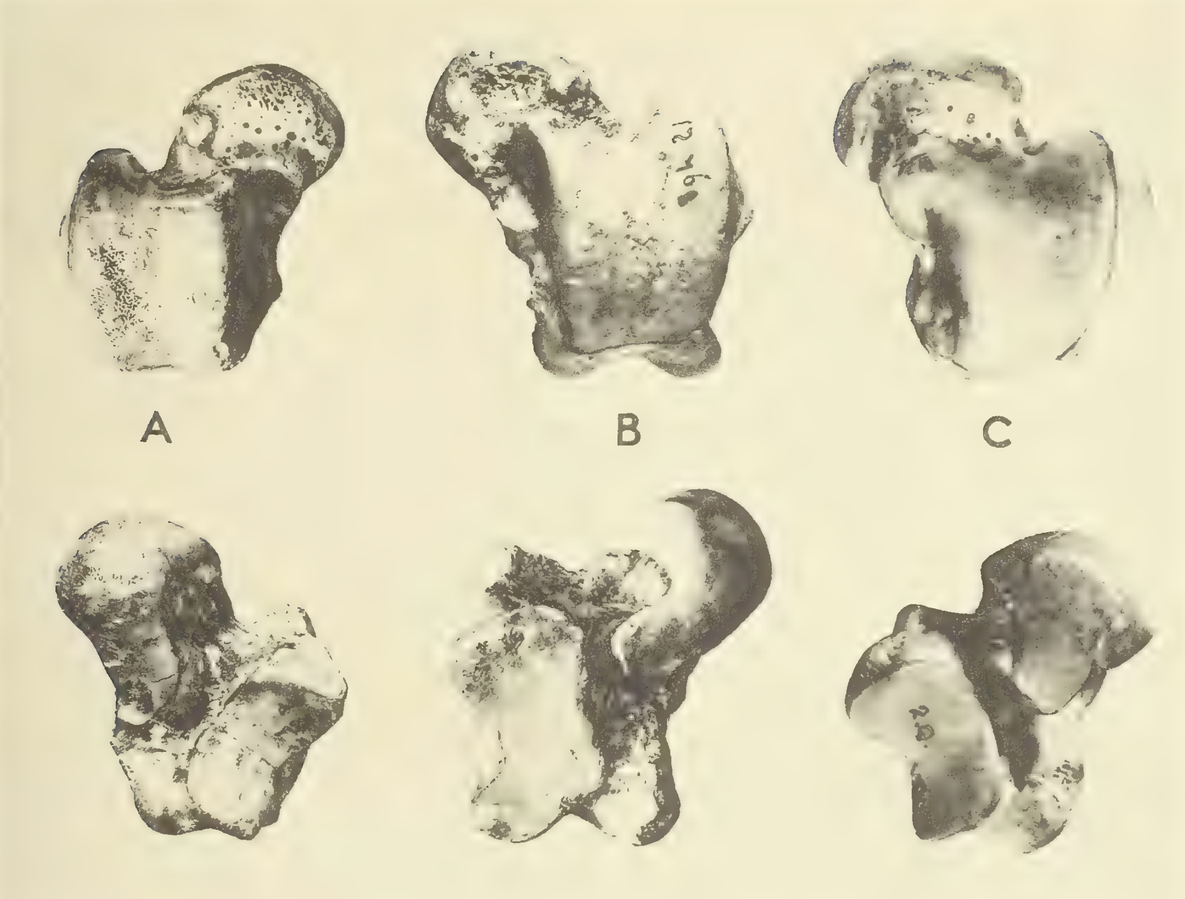
EXPLANATION OF PLATE VIII

All figures natural size

FIG. 64. (a) Left talus (C.M.H.147), and (b) right talus (C.M.H.145), provisionally referred to *Proconsul ?nyanzae*. For comparison the talus of an adult male chimpanzee (c) is also illustrated. Above, the tali are viewed from the dorsal aspect, and below from the plantar aspect.

,, 65. Right calcaneum (C.M.H.146) associated with the talus (C.M.H.145) shown in the previous figure, viewed from the medial aspect. In this and the following illustrations, an outline of the calcaneum of an adult male chimpanzee is shown for comparison, drawn to the same scale.

,, 66. The same specimen as that shown in the previous figure, viewed from the lateral aspect.



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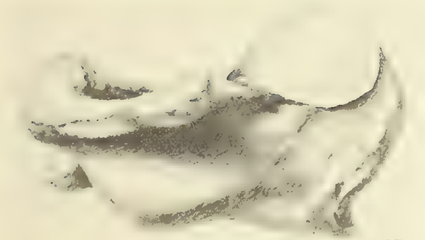

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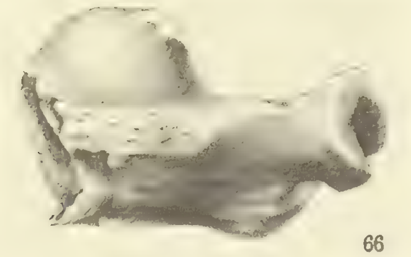

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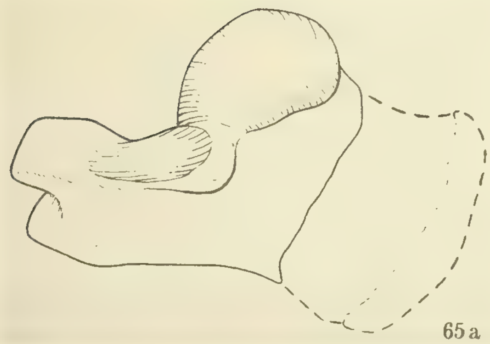

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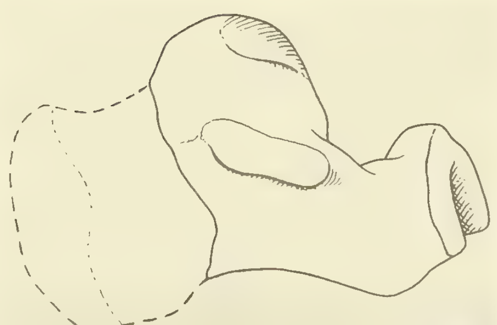


66 a

LIMB BONES OF PRIMATES

PLATE IX

EXPLANATION OF PLATE IX

FIG. 67. The same specimen as that shown in fig. 65, viewed from the dorsal aspect. Natural size.

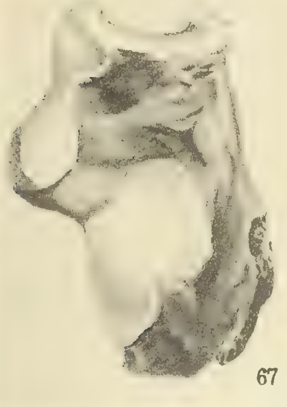
,, 68. The same specimen as that shown in fig. 65, viewed from the plantar aspect. Natural size.

,, 69. The upper end of a left femur found on Maboko Island, and provisionally attributed to *Proconsul*, viewed (a) from the anterior, and (b) from the posterior aspect. Reference should be made to text-fig. 23A, which illustrates the right femur of the same individual. Natural size.

,, 70. The upper end of a right femur found on Rusinga Island close to the fragment of a mandible (C.M.H.5) of *Proconsul nyanzae*, viewed from the posterior aspect. Natural size.

,, 71. Left talus of a small primate (B.3) found on Rusinga Island, viewed (a) from the dorsal, and (b) from the plantar aspect. × 1·5.

,, 72. Right talus of a small primate (B.2) found on Rusinga Island, viewed (a) from the dorsal, and (b) from the plantar aspect. × 1·5.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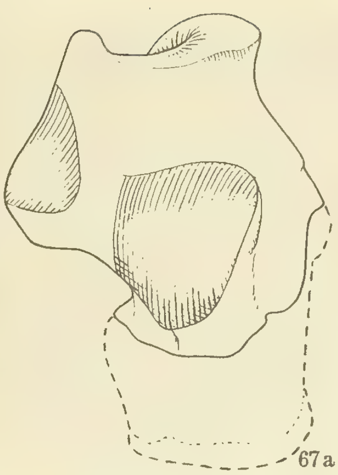
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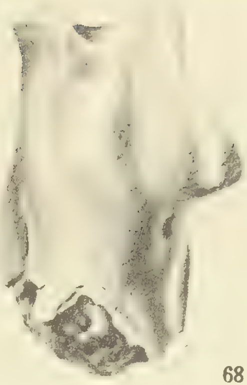
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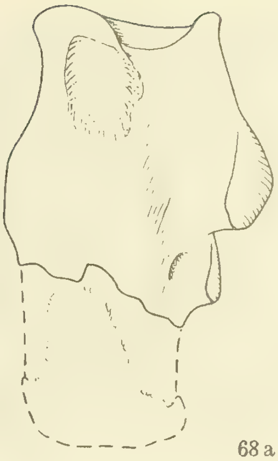
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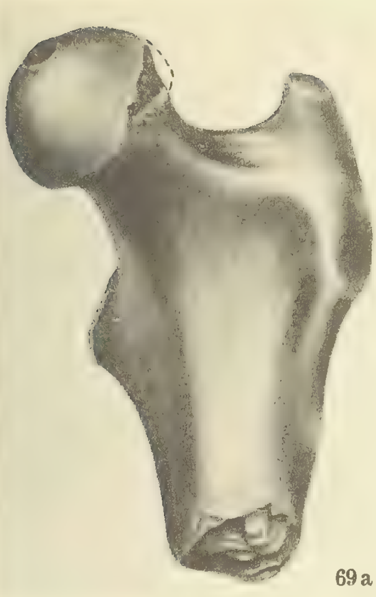
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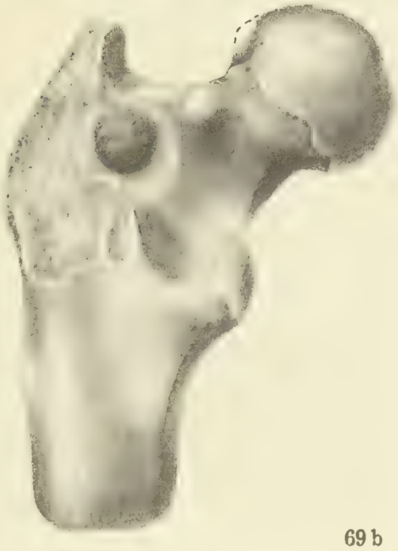
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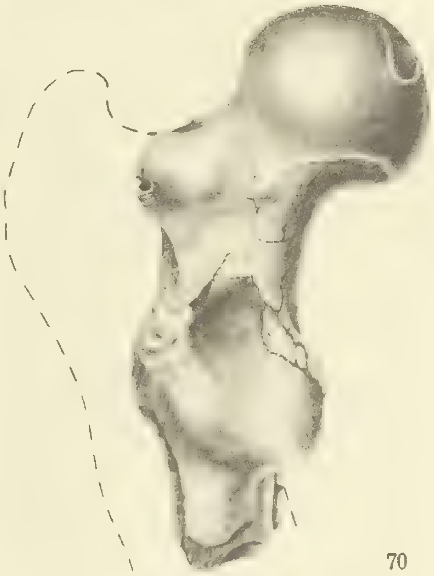
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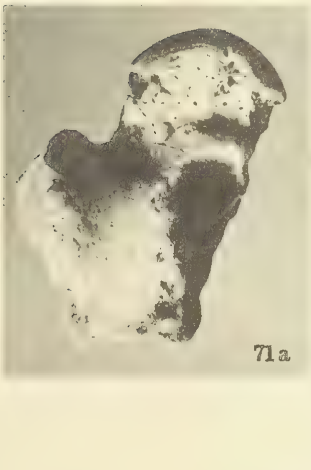
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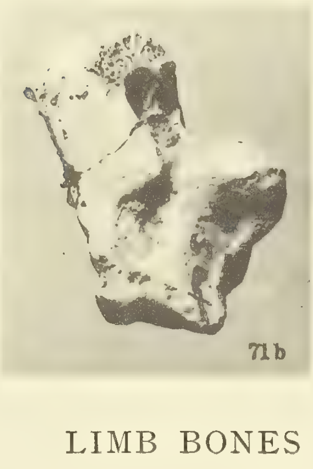
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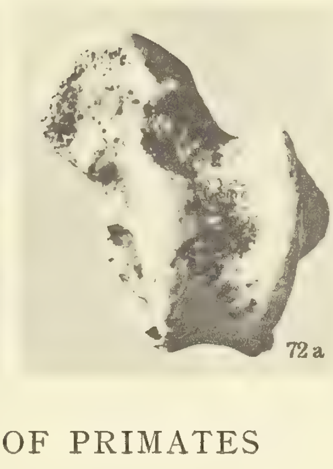
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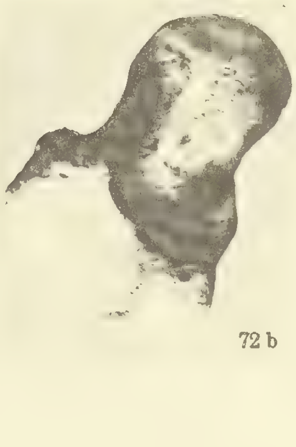
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LIMB BONES OF PRIMATES

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